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Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

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Fishery Bulletin

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EFFECTS OF TEMPERATURE AND SALINITY ON FERTILIZATION, EMBRYONIC DEVELOPMENT, AND HATCHING IN *BAIRDIELLA ICISTIA* (PISCES: SCIAENIDAE), AND THE EFFECT OF PARENTAL SALINITY ACCLIMATION ON EMBRYONIC AND LARVAL SALINITY TOLERANCE[1]

ROBERT C. MAY[2]

ABSTRACT

Eggs and larvae of the sciaenid fish bairdiella, *Bairdiella icistia*, were obtained from fish matured in the laboratory by photoperiod manipulation and induced to spawn by hormone injections. The effects of temperature and salinity on fertilization, embryonic development, hatching, and early larval survival were studied with the material thus obtained, and the effects on gametes of parental salinity acclimation were also investigated. Fertilization took place over a wide range of temperatures and salinities, but was completely blocked at salinities of 10‰ and below. A low level of spermatozoan activity may have accounted for the lack of fertilization at low salinities. Successful embryonic development occurred between temperatures of approximately 20° and 30°C, and salinities of 15 and 40‰. The production of viable larvae was estimated to be optimal at a temperature of 24.5°C and a salinity of 26.6‰. An interaction of the two factors was apparent, development at high salinities being most successful at low temperatures and development at high temperatures being most successful at low salinities. The stage of maturity of the spawning female had a great influence on the overall viability of the eggs produced, as well as on their response to temperature and salinity. Adult bairdiella matured sexually in dilute seawater with a salinity of 15‰, and the salinity tolerance of the eggs produced by these fish was unaltered.

The bairdiella, *Bairdiella icistia* (Jordan and Gilbert), is a sciaenid fish native to the Gulf of California. In 1950 the species was successfully introduced into the Salton Sea, a large saline lake in southern California (Whitney 1961). Salton Sea water has an ionic composition different from that of ocean water (Carpelan 1961; Young 1970), and its overall salinity, now approximately 38‰,[3] is rising at a rate of about 1‰ every 3 yr (U.S. Department of the Interior and the Resources Agency of California 1969). This rising salinity has caused concern that the present sport fishery in the Salton Sea (based on several fish species, including bairdiella) will fail when the upper salinity tolerances of the fishes are exceeded (Walker et al. 1961). Lasker et al. (1972) found that the survival of bairdiella eggs and early larvae was severely inhibited by Salton Sea water at a salinity of 40‰; thus, at the present rate of salinity increase, the bairdiella population may suffer a loss in recruitment within the next 10 yr.

The work reported in this paper was undertaken to provide more information on the salinity tolerance of bairdiella during early development, especially as influenced by temperature and by the acclimation of spawning parents to different salinities. Because of poor embryonic and larval survival in Salton Sea water (May 1972), these experiments were all conducted in seawater of ordinary ionic composition. The effects of Salton Sea water per se and their implications for the population of bairdiella in the Salton Sea will be discussed elsewhere (May in preparation).

Bairdiella normally spawn during April and May in the Salton Sea (Whitney 1961; Haydock 1971). However, thanks to the work of Haydock (1971), bairdiella can be induced to mature and spawn in the laboratory at any time of the year,

[1]Based on a portion of a dissertation submitted in partial satisfaction of the requirements for the Ph.D. degree at the University of California at San Diego, Scripps Institution of Oceanography.

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[3]This value varies somewhat with season and location in the Salton Sea.

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making bairdiella eggs and larvae extremely favorable material for experimentation. In addition to providing a year-round supply of eggs, laboratory spawning techniques have permitted maintaining bairdiella at different salinities during maturation and spawning in order to test the effect of parental salinity acclimation on the salinity tolerance of the gametes, embryos, and larvae.

MATERIAL AND METHODS

Capture and Maintenance of Fish

Methods used for collecting and maintaining bairdiella were nearly identical to those described by Haydock (1971). Adult bairdiella were captured with a 60-m beach seine on the west coast of the Salton Sea, just north of the Salton Bay Yacht Club. Rectangular fiberglass tanks of 2,000-liter capacity were used to hold fish in the laboratory and were supplied with continuously flowing warm (22°C) seawater from the Southwest Fisheries Center system (Lasker and Vlymen 1969). Water was filtered through polypropylene GAF[4] snap-ring filter bags of 50-μm pore size (GAF Corp., Greenwich, Conn.). Mercury lamps provided illumination (Haydock 1971) and the photoperiod was controlled as desired by timers.

The fish were fed ad libitum twice each day with ground squid, supplemented by ground red crab, *Pleuroncodes planipes*, at a ratio of approximately 1 part of crab to 6 of squid (wet weight). The red crabs were intended as a source of carotenoids because some authors have indicated that parental carotenoid deficiency may affect the viability of offspring (Hubbs and Stavenhagen 1958).

Several outbreaks of the parasitic ciliate, *Cryptocaryon irritans* Brown, occurred (Wilkie and Gordin 1969) and were effectively controlled by adding copper sulfate at 0.2 ppm as Cu^{2+} in the morning and late afternoon, allowing the chemical to be diluted in the interim by the continuously flowing seawater. Whenever fish were handled, they were subsequently treated with Furacin antibiotic (Eaton Veterinary Laboratories, Norwich, N.Y.) at 130 ppm, which was gradually diluted in the open seawater system. This precaution effectively controlled bacterial infections and allowed repeated handling of fish without adverse consequences.

Induced Maturation and Spawning

Fish which had ripe gonads when captured were maintained in this condition for several months by exposing them to a photoperiod of 16 h light, 8 h darkness (16L:8D) at approximately 22°C (Haydock 1971). Prolonged exposure of female fish to long days resulted in eventual resorption of the ova. After a group of fish had been spawned out or had begun gonadal resorption, they were shifted to a short photoperiod (9L:15D) and colder water (15°C). After being held on short days for a few months, fish could then be brought to maturity by increasing the photoperiod at a rate of 30 min per day until 16L:8D was reached; after about 3 mo on 16L:8D at 22°C, the fish had developed mature ovaries and were ready to spawn. Successful spawning could be induced over a period of at least two or three more months before gonadal resorption began. Photoperiod manipulation was effective in inducing ovarian maturation regardless of the time of year, and the experiments described in this paper were conducted in the summer, fall, and winter instead of during the normal spring spawning period.

Bairdiella kept in the laboratory vary considerably in their ovarian development (Haydock 1971). In the present study the maturity of female fish was assessed from ovarian biopsies taken with a glass capillary tube (Stevens 1966). At first only the maximum oocyte diameters were recorded immediately after sampling, along with qualitative notes concerning the amount of ovarian stroma in the sample. When it became apparent that this was not a sufficiently sensitive measure of the state of maturity, the samples were preserved in 3% Formalin (in 50% seawater) and all oocyte diameters of 175 μm or greater were measured with an ocular micrometer a day or so later,[5] giving an oocyte size-frequency distribution based on measurements of approximately 100 oocytes. The fish which had been biopsied in this manner were marked individually on the lower jaw with injections of the dye, National Fast Blue 8GXM (= Fast Turquoise PT) (Kelley 1967; Haydock 1971).

Mature female fish weighing 100-150 g were injected in the epaxial musculature near the dorsal fin with 100 IU of gonadotropin from pregnant mare's serum (PMS; Sigma Chemical Co., St. Louis, Mo.) in a carrier of Ringer's solution, after

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]No measurable oocyte shrinkage occurred even after a week of preservation.

being anesthetized with MS-222 (tricaine methanesulfonate) at 150 ppm. Haydock (1971) found that salmon pituitary glands and PMS were both effective in inducing ovulation in bairdiella. PMS was used here because it had a standardized activity and was more readily available and easier to prepare than salmon pituitaries. The injected fish were checked for ovulation 30 h after injection and at hourly intervals thereafter until ovulation took place (Haydock 1971). In the vast majority of cases, ovulation occurred 30 or 31 h after the hormone injection. Spawning bairdiella of the size used in these experiments will yield 100,000 or more eggs (Haydock 1971). Male fish remained in a running ripe condition in the laboratory and did not require hormone injections. Bairdiella do not spawn spontaneously in captivity, whether injected or not, and gametes must be obtained by stripping. Haydock (1971) demonstrated that eggs must be fertilized 1 or 2 h after ovulation if maximal viability is to be retained.

Fertilization

Approximately 1,000 to 3,000 eggs were squeezed from an anesthetized, freshly ovulated female and added to a petri dish containing 75 ml of water of the desired temperature and salinity. When fertilizations under a number of conditions were to be made, eggs were added to all petri dishes before sperm was added. Sperm from a lightly anesthetized male fish was taken up in a pasteur pipette which was immediately filled and flushed with water from a petri dish containing eggs. Eggs and sperm were swirled in the dish for several seconds. This procedure was repeated for every dish, fresh sperm being obtained each time. After cleavage had begun, random samples (usually 100 to 300 eggs) were taken from each petri dish, preserved in 3% Formalin and later examined, and the number cleaving recorded. The percentage of eggs cleaving was taken as the percentage fertilized.

Spermatozoan activity was measured in various salinities by placing a drop of sperm under a cover slip, focusing on it with a compound microscope at 430× and adding seawater of the desired salinity. At frequent intervals after hydration, the activity of spermatozoa was rated on an arbitrary scale of 0 to 5, 0 being no activity and 5 being maximal activity. All such tests were conducted at approximately 25°C. More than 70 runs were made utilizing spermatozoa from nine fish, each run comprising between 4 and 15 observations, depending on the duration of activity.

Incubation

Developing eggs from the fertilization dishes were counted out by pipette under a dissecting microscope, rinsed with clean water of the test salinity to remove sperm, and transferred to incubators. The transfer of eggs was usually completed by the time the blastula stage had been reached, within 3 or 4 h after fertilization. One hundred developing eggs were placed in each incubator, and there were two replicate incubators for each experimental treatment. Each incubator (Figure 1) consisted of a 400-ml Pyrex beaker with an insert made from a truncated polypropylene beaker with its bottom covered by Nitex nylon mesh (350-μm mesh opening). Three hundred milliliters of water were added to each incubator. A slow stream of air bubbles in a centrally positioned glass tube created a flow of water such that eggs which rested on the bottom at low salinities were bathed by a continuous flow of aerated water (Figure 1).

One or two days before each experiment, seawater with a salinity of approximately 60‰ was made by adding artificial sea salts ("Instant Ocean"; Aquarium Systems, Inc., Wickliffe, Ohio) to HA Millipore-filtered seawater. This solution was filtered through paper (Whatman No. 1) to eliminate a residual cloudiness and then diluted with deionized water to the desired test salinities. Batches of seawater were aerated for several

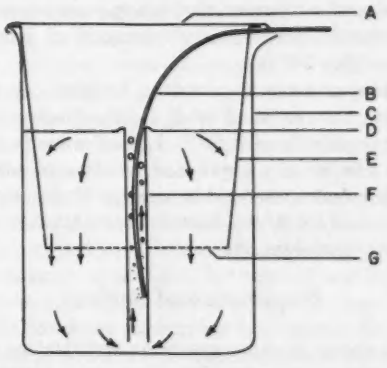

FIGURE 1.—Egg incubator. A) Parafilm cover; B) polyethylene air tube; C) 400-ml Pyrex beaker; D) water line; E) 250-ml polypropylene beaker, cut off at bottom; F) glass chimney; G) Nitex mesh. Arrows indicate direction of water flow.

hours before each experiment to stabilize oxygen tension and pH. Potassium penicillin G (50 IU/ml) and streptomycin sulfate (0.05 mg/ml) were added to the water just before it was placed in the incubators. Salinities were calculated by multiplying chlorinity values (Schales and Schales 1941) by 1.80655 (Johnston 1964) and remained within ±0.5‰ of the original salinity during an experiment. Temperatures were maintained within ±0.2°C of the desired values by immersing petri dishes and incubators in water baths equipped with cooling coils and thermostatically controlled heaters. The incubators were illuminated continuously from fluorescent room lamps which gave an intensity of from 320 to 480 lx at the water surface. Dissolved oxygen concentration in the incubators decreased with increasing temperature and salinity, and measured concentrations were within 2 or 3% of the saturation values given by Kinne and Kinne (1962). The highest oxygen content (at 18°C and 15‰) was 6.24 ml/liter, and the lowest (at 30°C and 55‰) was 4.05 ml/liter. The pH in the incubators increased with increasing salinity and decreasing temperature, varying between 8.08 and 8.27.

The percentage hatching and the condition of the larvae at hatching were recorded for each incubator. Supplementary containers (20-ml petri dishes) with 30 fertilized eggs each, were provided at each treatment to allow examination of eggs during development without disturbing the eggs in the incubators. Hatched larvae were not fed; some were kept in 400-ml beakers (without the polypropylene inserts used prior to hatching) and the pattern of mortality of the starved larvae recorded, and some were used in experiments on the temperature and salinity tolerance of yolk-sac larvae (May 1972).

During an early experiment, histological preparations were made of newly hatched larvae from different salinities at 25°C. Larvae were fixed in Bouin's solution, dehydrated in ethanol-normal butyl alcohol, embedded in paraffin, and sectioned transversely at 8 μm. Sections were stained with Mayer's hemalum and eosin.

Experimental Series

Two series of experiments on fertilization success, embryonic development, and hatching success were conducted, each series involving observations at 25 different combinations of temperature and salinity. Each series included two separate hormone-induced spawnings of fish held under identical conditions. The two spawnings in each series constituted a composite factorial array of treatments (a 3 × 5 plus a 2 × 5 factorial); this design, similar to those employed by Alderdice and his colleagues (Alderdice and Forrester 1967, 1971a, b; Alderdice and Velsen 1971), allowed coverage of a large factor space without utilizing all possible combinations of treatments. The ranges of temperature and salinity employed covered the viable ranges for bairdiella eggs, as determined in preliminary experiments. Table 1 indicates the temperatures and salinities in which eggs were fertilized and incubated in the two spawnings of each series.

The fish utilized for Series A were captured toward the end of the spawning season in the Salton Sea on 7 June 1971 and maintained on a 16L:8D photoperiod in 22°C water until the first hormone-induced spawning of the series on 23 August 1971 and the second on 1 September 1971. Ovarian biopsies indicated that the eggs were ready for spawning at this time, but only maximum oocyte diameters were measured and no oocyte size-frequency distributions were obtained. The tests were repeated in a second series of experiments, Series B. A group of fish captured in the Salton Sea on 20 May 1970 was shifted gradually

TABLE 1.—Dates and temperature-salinity conditions for experiments in Series A and B, 1971. There were two spawnings, performed at different dates, in each series; each spawning utilized eggs and sperm from different fish.

Temperature (°C)	Salinity (‰)	Series A		Series B	
		23 Aug.	1 Sept.	25 Nov.	3 Dec.
18	10	x		x	
	20	x		x	
	30	x		x	
	40	x		x	
	50	x		x	
21	15		x		x
	25		x		x
	35		x		x
	45		x		x
	55		x		x
24	10	x		x	
	20	x		x	
	30	x		x	
	40	x		x	
	50	x		x	
27	15		x		x
	25		x		x
	35		x		x
	45		x		x
	55		x		x
30	10	x		x	
	20	x		x	
	30	x		x	
	40	x		x	
	50	x		x	

from a short photoperiod to a 16L:8D photoperiod between 25 June and 10 July 1971. Half of these fish were transferred gradually to 15‰ and allowed to mature in that salinity as described below, while the other half were kept in seawater (approximately 33‰) and used to supply eggs for the Series B experiments. Prior to these spawnings, ovarian biopsies were taken and oocyte size-frequency distributions determined to assure that the fish were fully mature.

Acclimation of Spawning Fish to Low Salinity

These fish came from the same collection as those used to supply eggs in the Series B experiments and were brought to maturity simultaneously with them. The salinity was lowered to 15‰ over a period of 8 days by mixing seawater with an increasing proportion of fresh water. The day length was then increased from 9 to 16 h in 30-min increments, and the temperature was raised from 16° to 22°C over the same period (Figure 2). The tap water had been dechlorinated by passage through a commercial charcoal filter, and the mixed tap water and seawater flowed through the fish tank at 1,000 liters per hour (the same flow rate was maintained in the tank receiving straight seawater). Salinity was monitored daily in the seawater and low-salinity tanks. Variations were relatively slight during the period of gonadal maturation, monthly means ranging from 32.7 to 33.3‰ in the seawater tank and from 15.2 to 15.7‰ in the low-salinity tank.

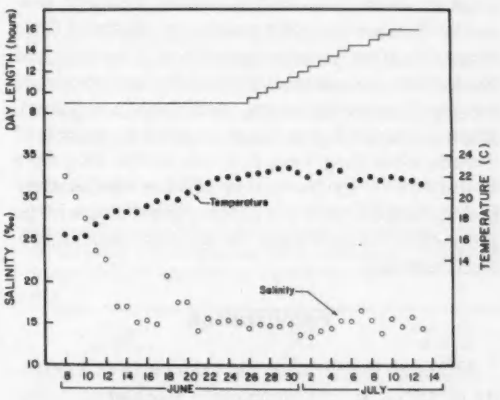

FIGURE 2.—Day length, temperature, and salinity during transition period, when fish were transferred to low-salinity water, warm temperatures, and long days.

Female fish living at 15‰ were injected with PMS on 25 October, 8 November, and 16 November 1971. Eggs were fertilized (with sperm from males also acclimated to 15‰) and incubated as described above, at salinities of 10, 15, 20, 30, 40, 45, and 50‰. The temperature was 24.0°±0.2°C in all experiments with eggs from fish acclimated to low salinity. Hatched larvae were kept in 400-ml beakers at their original salinity to determine the percentage surviving to yolk exhaustion. The activity of spermatozoa from fish acclimated to 15‰ was assessed at various salinities as described above.

RESULTS

Spermatozoan Activity

Bairdiella spermatozoa measured 40 μm in total length, the head being about 2.5 μm long. In distilled water and dechlorinated tap water, spermatozoa showed at most only slight movement, usually in the form of very slow undulations which lasted at least 10 min. After approximately 1 min, the heads of many of these spermatozoa seemed to acquire bright rings, which an oil-immersion lens revealed to be the tail curled around the head, still undulating slowly.

Bairdiella spermatozoa became activated immediately upon contact with seawater (Haydock 1971), and the intensity of activity varied with salinity and time after initial contact with water. Spermatozoa were most active at the higher salinities but remained active longest at the lower salinities. At 10 and 15‰, a small smount of activity remained even as long as 10 min after hydration, but at 10‰ spermatozoa seldom showed activity above level 3 and at 15‰ they only rarely and briefly attained level 5 (Figure 3). At 25‰ all activity ceased by 4 min after hydration, and at 35‰ no activity was usually seen after 3 min. At 45 and 55‰, activity had completely stopped by 1.5 min after hydration. On rare occasions, at salinities between 15 and 55‰, slow undulations of some spermatozoa were observed after other movements had ceased. No difference was noted between spermatozoan activity in seawater and in Salton Sea water, nor between the activity of spermatozoa from fish acclimated to a salinity of 15‰ and from those kept at 33‰. Spermatozoan activity in dilute suspensions of

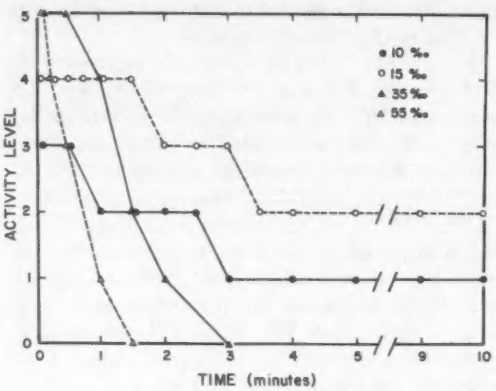

FIGURE 3.—Spermatozoan activity in four salinities as a function of time after hydration. The activity levels are described in the text.

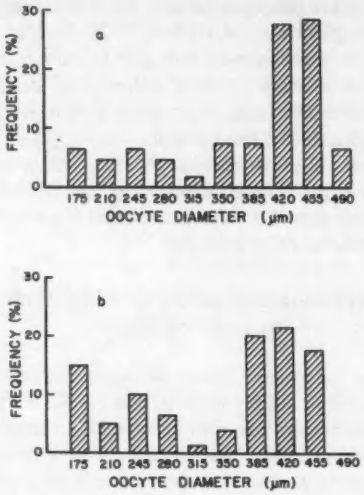

FIGURE 4.—Oocyte size-frequency distributions, based on ovarian biopsies, from fish used in Series B experiments. a) fish spawned on 25 November 1971, b) fish spawned on 3 December 1971.

sperm was the same as when hydration was carried out underneath a cover slip, indicating that the high concentration of spermatozoa in the latter case did not seriously affect the level or duration of their activity.

Maturity of Spawning Fish

Examination of many fish during this project showed that 500 μm was approximately the maximum diameter attained by oocytes in bairdiella before gonadal hydration. During hydration, which occurs in the laboratory only after an injection of gonadotropic hormone, the accession of water swells the eggs to 700 μm or more, the size at spawning. Ovarian biopsies showed that the two female fish used to supply eggs in the Series A experiments had oocytes as large as 500 μm before injection. The oocyte size-frequency distributions for the fish used in Series B (Figure 4) also showed maximum diameters of about 500 μm, and there were modes at 420 to 455 μm for the first fish and 385 to 455 μm for the second in Series B.

The much poorer fertilization and hatching success in Series A (see below) indicates that maximum oocyte diameter is not necessarily a good index of readiness for spawning. By this method it is impossible to tell whether there is a mode at the large end of the size-frequency distribution, as is characteristic of fish which are ready to spawn. The fish used to supply eggs in Series A were probably captured after the peak of spawning in the Salton Sea and their gonads at that time were probably either partly spent or beginning to be resorbed (see Haydock 1971). It was hoped that subsequent exposure to long days would induce ovarian recrudescence, but instead this treatment over a period of 2.5 mo apparently maintained the gonads at a suboptimal state of maturity or allowed them to regress even further (see Haydock 1971). A postspawning refractory period (Harrington 1959; Sehgal and Sundararaj 1970) may exist in bairdiella, but it cannot be very pronounced, since not only were eggs obtained from these fish after hormone injections in August and September, but at least 60% of the eggs could be fertilized under optimum conditions (see below). The fish used in Series B had completely regressed gonads when they were first exposed to long days in July 1971. By November 1971 or earlier they had developed ovaries capable of producing a large proportion of viable eggs, showing as much as 90% fertilization.

Fertilization

Although fertilization did take place at a salinity of 15‰, it was completely blocked at 10‰ (Table 2). In order to examine this phenomenon further, unfertilized eggs were placed in 10‰ water for various periods of time and then trans-

TABLE 2.—Percentage fertilization at various combinations of temperature and salinity in Series A and B.

Temperature (°C)	Salinity (‰)	Percentage fertilization	
		Series A	Series B
18	10	0	0
	20	14.5	28.9
	30	48.5	81.6
	40	24.4	87.5
	50	14.8	41.6
21	15	13.4	18.4
	25	43.5	69.9
	35	35.8	49.4
	45	36.8	59.9
	55	1.9	52.5
24	10	0	0
	20	63.1	62.3
	30	43.2	87.8
	40	7.4	81.3
	50	5.7	50.8
27	15	33.7	30.3
	25	52.6	77.2
	35	60.1	76.7
	45	16.8	82.0
	55	0	67.4
30	10	0	0
	20	48.7	74.6
	30	15.3	89.8
	40	2.7	68.7
	50	0	23.1

ferred to 20‰ and immediately exposed to sperm. The results (Table 3) showed that 10‰ water did not render the eggs infertile: even after 20 min at 10‰, a large proportion of the eggs could be fertilized at 20‰ and develop to hatching, although there was no fertilization in controls kept at 10‰. It was also found that eggs fertilized at 20‰ could be transferred to 10‰ and develop to hatching (Table 4). Thus the actual process of fertilization was somehow blocked at 10‰.

In Series A, fertilization was much more sensitive to high salinities and there seemed to be a greater temperature-salinity interaction than in Series B, with fertilization being more successful at high salinities when the temperature was low (Table 2). In Series B, at salinities above 10‰,

TABLE 3.—Effect of exposure to 10‰ water for various periods of time on fertilizability of bairdiella eggs at 20‰. At each time interval, between 200 and 400 eggs were transferred from 10 to 20‰, exposed to sperm, and later examined for fertilization. Thirty fertilized eggs from each group were followed until hatching.

Time at 10‰	Fertilized at 20‰ (%)	Hatching at 20‰ (%)
45 s	92.5	60.0
2 min	90.2	66.7
5 min	75.4	74.2
10 min	48.4	43.3
20 min	44.8	75.9

TABLE 4.—Survival and hatching of fertilized eggs transferred from 20‰ to 10‰ at various stages. Eggs were incubated in 20-ml petri dishes. The stages are described in Table 6.

Stage at transfer	Number of eggs transferred	Survival to stage VI (%)	Hatching (%)
IIe	30	96.7	63.3
IV	31	93.6	41.9
V	30	100	66.7
VII	29	—	62.1

fertilization was in nearly all cases over 50%, the few exceptions being at low temperature/low salinity and high temperature/high salinity combinations. A maximum of 89.8% fertilization was observed at 30°C-30‰ in Series B. The thermal limits for fertilization in Series B were evidently beyond the range tested (18°-30°C).

Normal Development

It will be helpful to outline the normal pattern of development of bairdiella eggs before discussing alterations in this pattern induced by various combinations of temperature and salinity. Newly spawned bairdiella eggs are approximately 725 μm in diameter and contain an oil globule with a diameter of about 18 μm. Occasionally there are two or three smaller oil globules instead of a single one. Like most pelagic eggs, bairdiella eggs float with the animal pole downward. The development of *Bairdiella icistia* eggs (Table 5, Figure 5) follows the pattern typical for small pelagic fish eggs and is not greatly different from that of *B. chrysura* as described by Kuntz (1915). Ahlstrom's numerical designation of developmental stages (Ahlstrom 1943) has been adopted here (Table 5), although some slight modifications of his scheme were necessary, and some of the stages have been broken down into substages. The times required to reach certain stages are listed (Table 5) for eggs at 33‰ at 25°C, based on observations made during a preliminary experiment in 1970. The newly hatched larvae are approximately 1.7 mm in length (snout to tip of notochord) and in ordinary seawater float upside down near the surface of the water.

Incubation Time

The time between fertilization and hatching varied with temperature and with salinity, and the patterns of hatching determined from the supplementary containers in Series B are shown in

TABLE 5.—Normal development of bairdiella eggs. Designation of stages in general follows Ahlstrom (1943), and times required to reach various stages are given for eggs in 33‰ water at 25°C.

Ahlstrom stage	Sub-stage	Approximate time after fertilization	Description
I	a	—	Unfertilized egg
	b	2 min	blastodisc
II	a	40 min	2 blastomeres
	b	50 min	4 blastomeres
	c	60 min	8 blastomeres
	d	2 h	Morula
	e	3 h	Blastula, periblast very apparent
III	a	6 h	Early gastrula, germ ring encircles as much as 1/3 of yolk, embryonic shield rudimentary
	b	7 h	Mid gastrula, embryonic shield expands, germ ring encircles as much as 2/3 of yolk
IV		8 h	Late gastrula, primitive streak forms
V		9 h	Blastopore closes, optic vesicles and Kupffer's vesicle form
VI	a	10 h	Somites begin to form; scattered melanophores appear, most dorsally behind optic vesicles, a few extending posteriad along notochord
	b	12 h	Lens and otic vesicles form, tip of tail reaches oil droplet
VII		15 h	Tail has moved beyond oil droplet and lifted off yolk; finfold apparent
VIII		17 h	Tail well beyond oil droplet; embryo twitches occasionally; heartbeat regular
—		20 h	Hatching

Figure 6. Series A showed similar patterns, but due to poorer survival the data are less complete and are not shown. In Figure 6 the cumulative percentage hatched has been plotted on a probability scale against time on an arithmetic scale; a straight line in this type of plot indicates a normal distribution (Sokal and Rohlf 1969), which is to be expected if differences in hatching time are due simply to random individual variation. At 30°C hatching was normally distributed for all salinities, but this was not true at the lower temperatures. At 27°C there was a plateau at 25‰, indicating that the hatching of certain eggs was delayed. At 24°C, hatching was distributed approximately in a normal fashion at 20, 40, and 50‰, but at 30‰ there was an inflection, the rate of hatching being slower after 23 h than before. At 21°C, hatching was distributed normally for 15, 35, and 45‰, but at 25‰ hatching took place in two phases separated by a 3-h period during which no hatching took place.

The time required for 50% of the larvae to hatch, estimated by graphical interpolation, decreased from 35.2 h at 21°C-25‰ to 16.0 h at 27°C-25‰. The estimated time at 50% hatching was slightly later at 30°C than at 27°C, although hatching began 2 h earlier in the former (see Figure 6). No clear-cut effect of salinity on median hatching times is discernible, but Figure 6 shows that hatching was completed more rapidly at the higher salinities (35‰ and above). The duration of hatching (the time between the appearance of the first and last hatched larvae) tended to be greater at the lower salinities and temperatures.

Embryonic Mortality

In certain treatments some surviving embryos failed to hatch but continued to develop within the chorion. Alderdice and Forrester (1971b) introduced the apt term, "postmature unhatched eggs" to describe such cases. Almost without exception, the postmature unhatched embryos were deformed in some way, usually bent and abnormally small. Often in such eggs part of the chorion was eventually digested away (Figure 7f), presumably by hatching enzymes, but the weak embryo was incapable of breaking completely free. Postmature unhatched eggs were most common at the low salinities, and the greatest proportion occurred at 30°C-20‰ (Table 6).

Eggs in Series A showed much higher mortality than those in Series B, especially at the higher temperatures and salinities (Table 7). The following description of embryonic mortality refers primarily to the eggs in Series B, which are considered more representative of normal, healthy eggs. The higher mortality in Series A usually showed up very early in embryonic development (prior to stage V); otherwise the two series showed similar trends.

No eggs hatched at 18°C and nearly all died during stage IIe (blastula). After the second cleavage at 18°C the blastomeres assumed a cloverleaf appearance which was not seen at higher temperatures (Figure 7; cf. Figure 5). Subsequent cleavages at 18°C were rather irregular, and during the blastula stage much of the cytoplasm gathered into isolated clumps, and the periblast became unusually large (Figure 7). Nearly all eggs stopped developing at this stage.

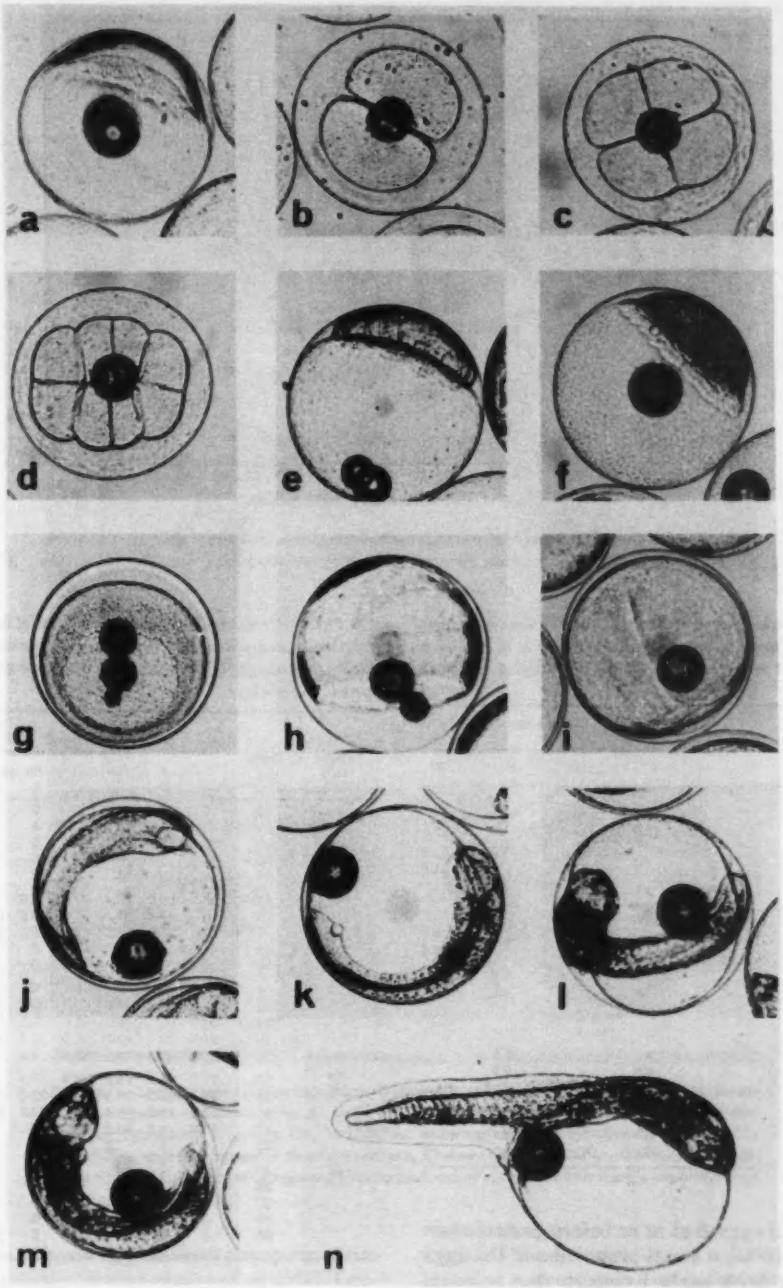

FIGURE 5.—Normal developmental stages of *Bairdiella icistia* at 25°C-33‰. a) stage Ib, 4 min after fertilization; b) stage IIa, 40 min; c) stage IIb, 50 min; d) stage IIc, 60 min; e) stage IId, 2 h; f) stage IIe, 3 h; g) stage IIIa, 6 h; h) stage IIIb, 7 h; i) stage IV, 8 h; j) stage V, 9 h; k) stage VI, 12 h; l) stage VII, 15 h; m) stage VIII, 17 h; n) newly hatched larva.

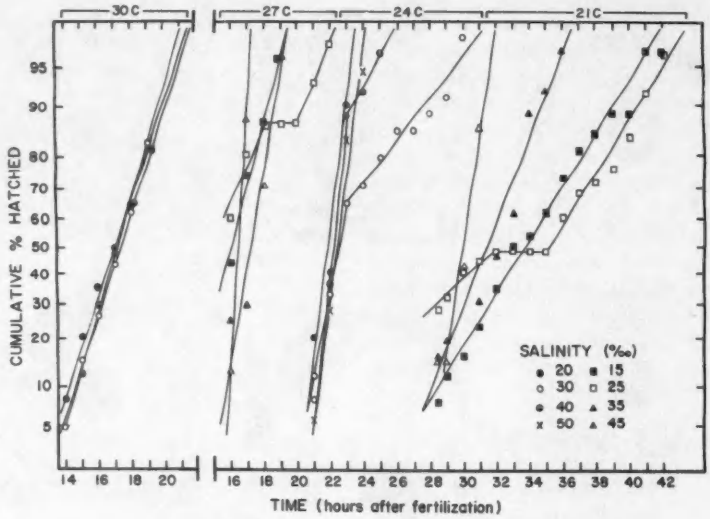

FIGURE 6.—Cumulative percentage of larvae hatching, as a function of time after fertilization, for the Series B experiments. Percentage hatching is plotted on a probability scale; lines were fitted by eye.

TABLE 6.—Percentage of postmature unhatched eggs at various combinations of temperature and salinity in Series B. There are two replicates at each treatment combination. Series A showed similar trends.

Salinity (‰)	Temperature (°C)			
	21	24	27	30
15	17.9		16.4	
	23.5		11.1	
20		19.2		43.4
		13.9		31.8
25	2.1		4.0	
	2.0		3.2	
30		7.8		6.7
		4.4		23.0
35	4.0		7.2	
	7.5		5.2	
40		0		3.1
		0		2.1
45	0		5.5	
	4.0		9.9	
50		0		0
		0.9		0
55	0		0	
	0		0	

TABLE 7.—Percentage total and viable hatch of fertilized eggs in various combinations of temperature and salinity in Series A and B. In each series there were two replicate groups of eggs (a and b) at each treatment combination.

Temperature (°C)	Salinity (‰)	Percentage total hatch				Percentage viable hatch			
		Series A		Series B		Series A		Series B	
		a	b	a	b	a	b	a	b
18	10	0	0	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0
	30	0	0	0	0	0	0	0	0
	40	0	0	0	0	0	0	0	0
	50	0	0	0	0	0	0	0	0
21	15	66.7	82.5	88.4	76.5	2.0	7.5	77.9	68.4
	25	25.0	40.4	94.7	92.9	20.0	29.3	77.9	59.7
	35	27.6	37.0	72.7	68.8	16.3	35.0	50.6	38.8
	45	1.9	7.1	72.8	47.5	0	2.0	18.1	11.9
	55	0	0	0	0	0	0	0	0
24	10	0	0	0	0	0	0	0	0
	20	62.6	39.8	96.0	96.0	33.3	23.5	70.0	80.2
	30	34.3	53.5	75.6	89.0	28.3	44.6	63.0	70.2
	40	24.2	51.4	66.3	80.0	10.1	38.3	34.6	53.8
	50	8.0	9.9	66.3	41.2	1.3	2.8	0	0
27	15	67.7	66.0	76.2	89.9	7.1	4.1	68.2	81.1
	25	22.6	34.1	79.8	88.4	22.6	30.6	70.8	81.0
	35	40.9	41.5	78.4	79.2	30.7	29.8	57.5	54.7
	45	11.9	4.5	42.9	31.9	0	1.5	0	0
	55	0	0	1.0	2.0	0	0	0	0
30	10	0	0	0	0	0	0	0	0
	20	12.0	14.4	85.9	73.8	7.0	3.1	38.2	28.6
	30	1.0	1.0	62.2	60.0	0	0	15.2	14.6
	40	0	0.9	4.1	6.2	0	0	0	0
	50	0	0	0	0	0	0	0	0

At 30°C, all eggs died at or before gastrulation at 50‰; at 40‰, a small proportion of the eggs survived the high early mortality but most of these failed to hatch, only 4-6% hatching successfully in Series B (Table 7). At 20 and 30‰ at 30°C, most embryonic mortality occurred after the embryos had developed pigmentation, although at 30‰ abnormal development was apparent in many eggs during cleavage and gastrulation

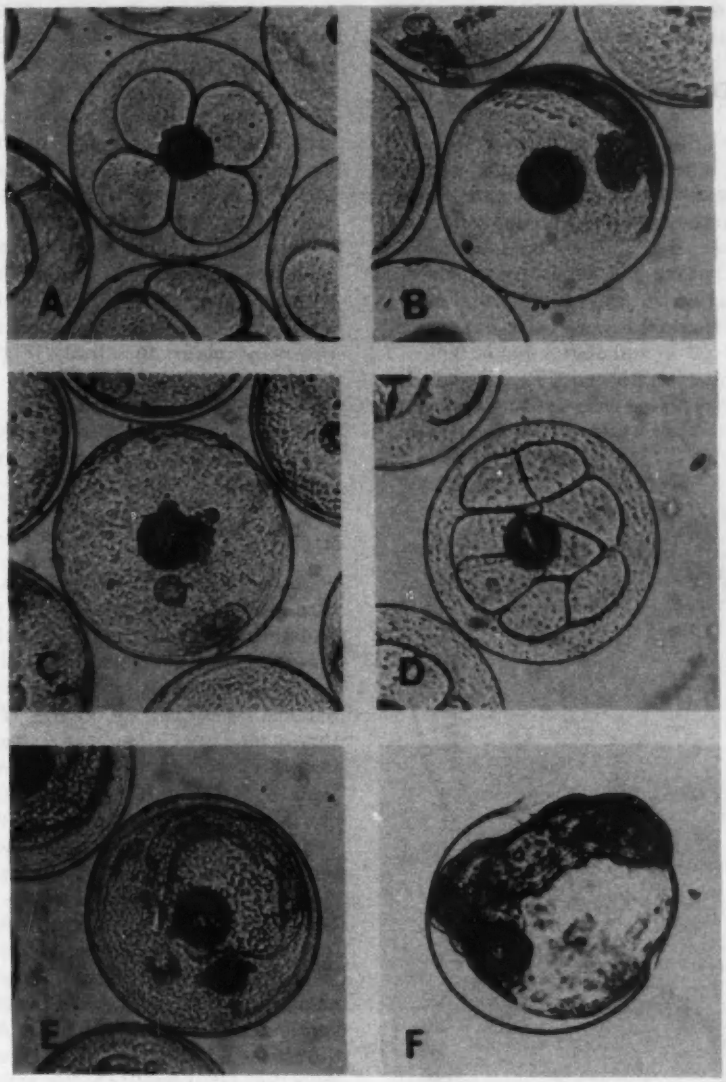

FIGURE 7.—Developmental abnormalities. A) stage IIb, at 18°C-30‰, showing unusual cloverleaf appearance of blastomeres; B) stage IIe, 18°C-30‰, showing enlarged periblast and clumped cytoplasm; C) stage IIe, 18°C-30‰, showing clumped cytoplasm; D) stage IIc, 30°C-30‰, showing irregular cleavage pattern; E) stage IIIa, 30°C-30‰, showing abnormal germ ring and clumping of cytoplasm; F) deformed embryo unable to free itself completely from the chorion, 24°C-20‰.

(Figure 7), and some eggs showed clumping of the cytoplasm similar to that observed at 18°C. Larvae hatching at 30°C were inactive. By following the development of individual eggs in the supplementary containers, it was noted that, no matter what the temperature or salinity, irregularly cleaving eggs usually died before completing gastrulation, and none ever hatched. At 21°, 24°, and 27°C, hatching was generally poorer at the higher salinities (Table 7). At 55‰ virtually no hatching

took place. A maximum of 96% hatching of fertilized eggs was observed at 24°C-20‰.

Deformed Larvae

Immediately after hatching, larvae often had curved bodies reflecting the curvature necessitated by confinement within the chorion (Figure 8), but such larvae soon straightened out. Some larvae, however, had sharply bent or kinked notochords at hatching, a deformity which was irreversible and which prevented normal swimming. These deformities were most common at high salinities (40‰ and above) and at 30°C. In Series A, salinities of 15 and 20‰ produced a high proportion of larvae with a strange deformation, in which the tail was recurved and fused to the trunk (Figure 8). Up to 78% of the larvae hatching at 27°C-15‰ showed this irreversible deformity in Series A, but the figure was only about 15% at 21°C-15‰ and less than 10% at 24°C-20‰; with one or two minor exceptions, other treatments in Series A did not produce this particular distortion, and it was not observed in any treatment in Series B. A greater proportion of late-hatching larvae in a given treatment displayed deformities than early-hatching larvae.

Larvae hatching at 15 and 20‰ showed pronounced edema (Figure 9). Histological sections showed that the size of the subdermal space was inversely related to salinity (Figure 10), an osmotic phenomenon which Battle (1929) also observed in larvae of *Enchelyopus cimbrius*. The yolk sac of newly hatched bairdiella larvae was larger and contained more water at lower salinities (May 1972).

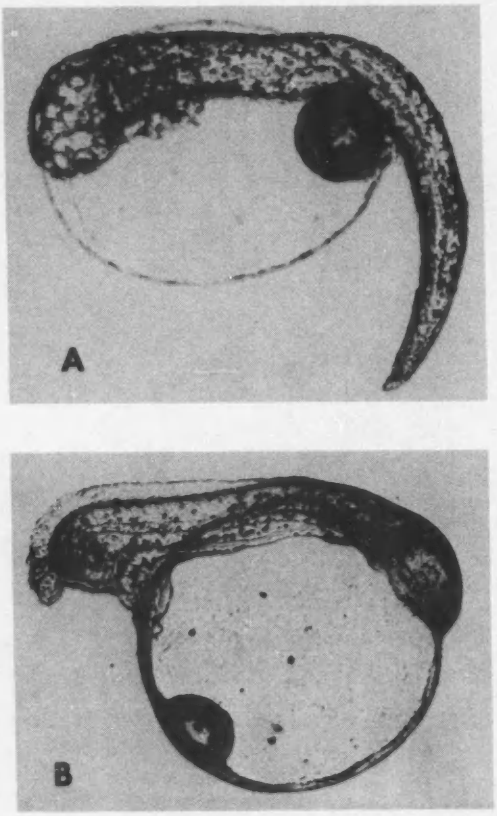

FIGURE 8.—Newly hatched larvae. A) ventral view of a normal larva, showing curvature often seen just after hatching, 24°C-30‰; B) lateral view of a larva with a recurved tail, 24°C-20‰, Series A.

Survival of Starved Larvae

Besides showing deformities, at high temperatures and salinities many larvae died before exhausting their yolk supplies. At 45 and 50‰ all larvae in Series A were dead within 1 day after hatching, and the same was true of the few hatched larvae at 40‰ at 30°C (Figure 11). The time of major mortality and the maximum survival time of starved larvae were inversely proportional to temperature and salinity. Because some of the larvae from Series B were used in tests of temperature and salinity tolerance (May 1972), a complete set of survival curves is not available for them. However, estimates of the percentage of larvae surviving to yolk absorption were obtained from the remaining larvae and from larvae in the least stressful conditions in the tolerance experiments, and these estimates indicated better larval survival in Series B than in Series A. For example, the Series B curves for 27°C (Figure 12) did not show the high mortality before yolk exhaustion at 25 and 35‰ seen in Series A, and a similar difference between the two series occurred at 21°C. At 24°C-40‰, an estimated 70% of the larvae were alive at yolk exhaustion in Series B, compared with only about 20% in Series A. At the highest temperatures and salinities, however, Series B showed heavy early mortality similar to Series A.

Viable Hatch

The percentage hatching of viable larvae (Table

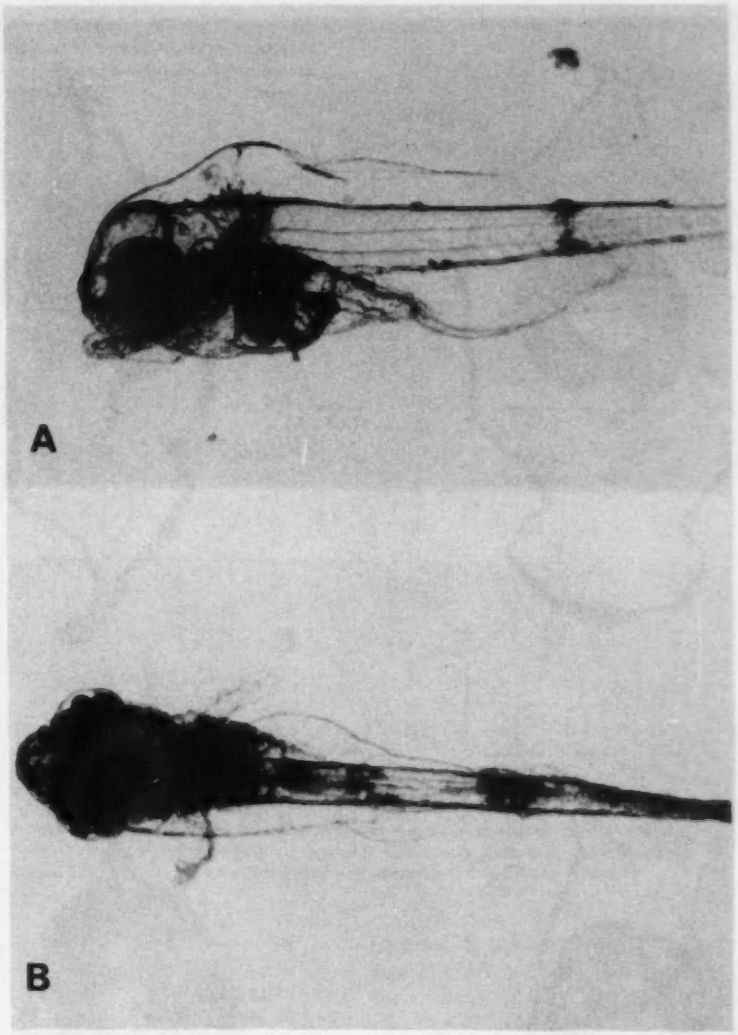

FIGURE 9.—Two-day-old larva, 24°C-20‰, with enlarged subdermal space. A) side view, B) dorsal view.

7), calculated from the preceding information, may be considered the ultimate criterion of successful development in these experiments. Viable larvae are defined here as morphologically normal larvae capable of surviving to yolk absorption, since all other larvae would not survive in nature. Series A showed a much lower viable hatch than Series B at very high and very low temperatures and salinities. Even for the best eggs, it is clear that salinities above 40‰ are detrimental to early survival, and that 30°C is extremely stressful. Survival at higher salinities was considerably better at low temperatures. The various observations on embryonic and larval survival in Series B are summarized (Figure 13) in the manner of Alderdice and Forrester (1967).

Response Surfaces

It has become customary to describe a biological

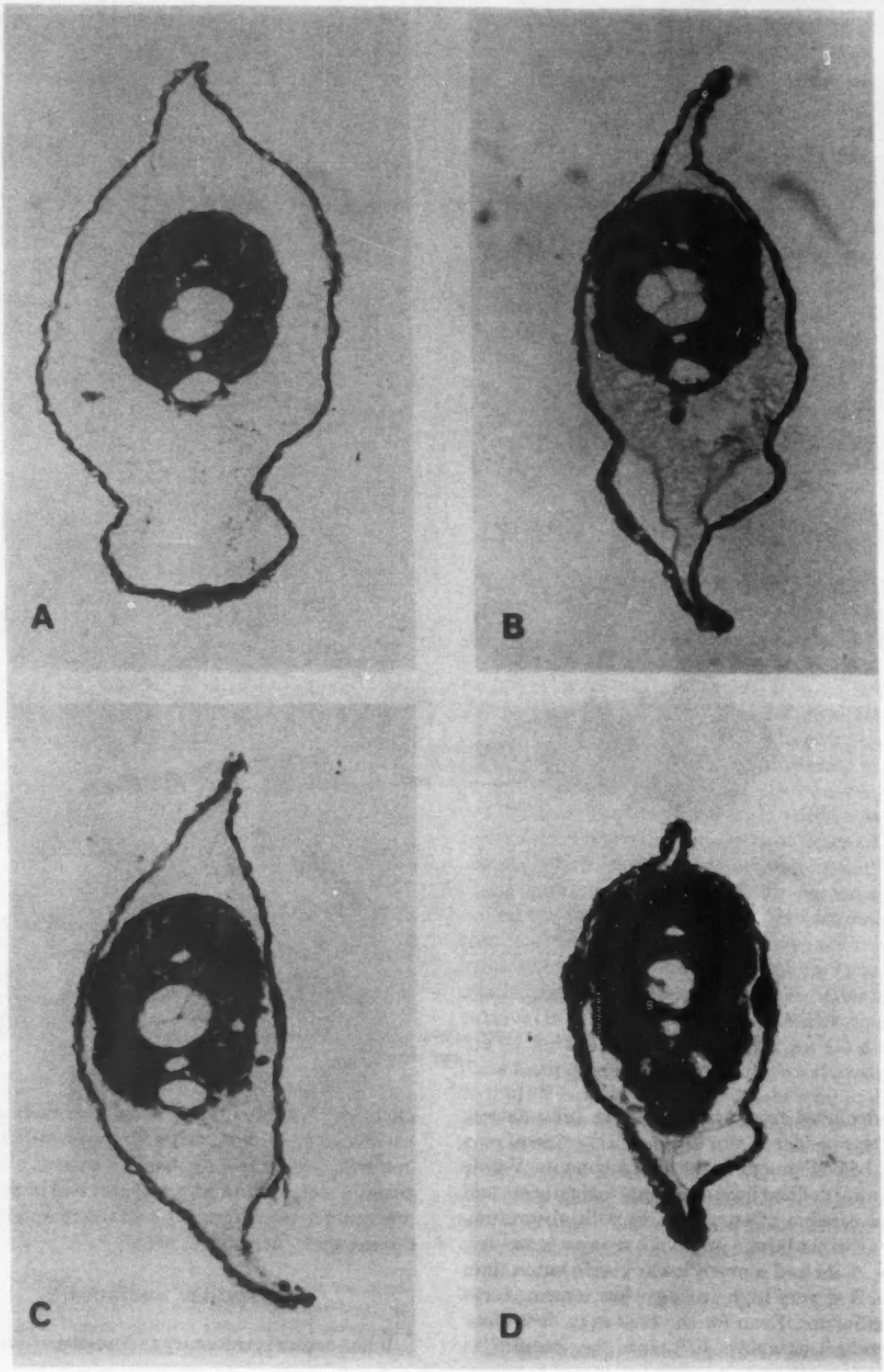
A
B
C
D

FIGURE 10.—Transverse sections of newly hatched larvae incubated in various salinities at 25°C. Serial sections were made of each larva, and the sections illustrated were located two sections posterior to the anus. A) 20‰, B) 33‰, C) 45‰, D) 50‰.

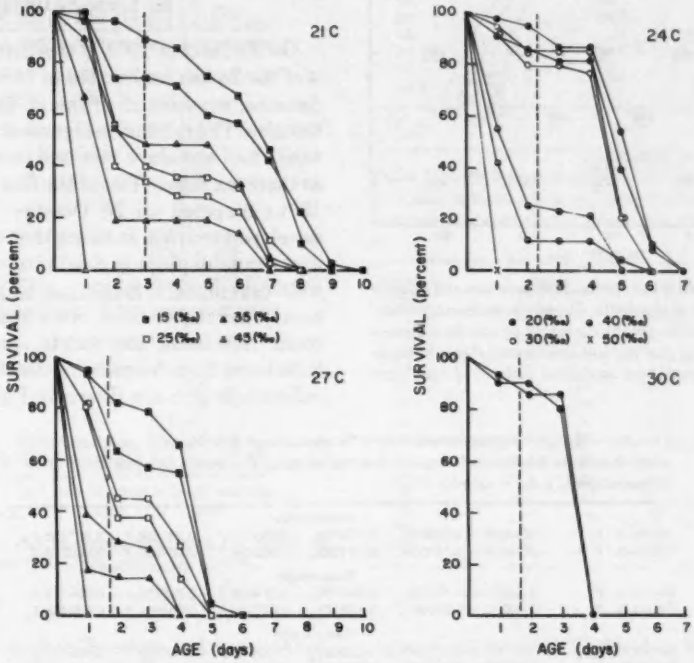

FIGURE 11.—Survival curves for unfed larvae at various temperatures and salinities in Series A. There were two replicate groups of larvae at each treatment, and the vertical dashed lines indicate the time of complete yolk absorption at each temperature.

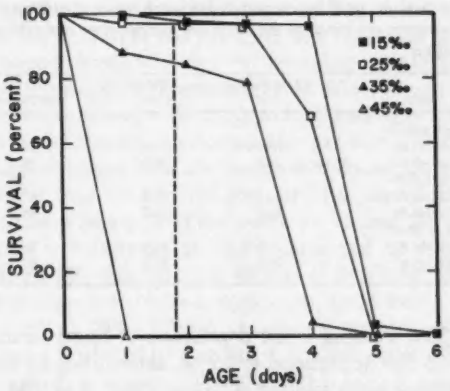

FIGURE 12.—Survival curves for unfed larvae in various salinities at 27°C, Series B. Vertical dashed line indicates the time of complete yolk absorption.

response to temperature and salinity by fitting a second order polynomial to the data and presenting response surfaces calculated from this equation (e.g., Costlow et al. 1960; Alderdice and Forrester 1967; Haefner 1969). This procedure was applied by computer to the results for fertilization, total hatch, and viable hatch, and the resulting equations are given in Table 8. Analysis of variance (ANOVA) showed that, although regression accounted for most of the variance in these data, deviations from regression were highly significant for all equations. This probably reflects the difficulty of fitting a second order polynomial to data of this sort, especially when abrupt thresholds are present, as between 10 and 15‰ and 18° and 21°C. A higher order polynomial, or a nonlinear model (Lindsey et al. 1970), would no doubt yield a better fit. Nonetheless, the second

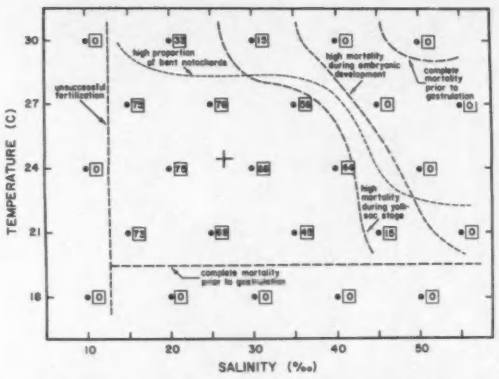

FIGURE 13.—Summary of the effects of temperature and salinity on early development of bairdiella. Closed circles identify treatment combinations utilized in the experiments, and the numbers in squares beside them give the mean values for viable hatch in Series B. The cross marks the estimated position of maximum viable hatch.

significance of interaction by existing statistical techniques.

Acclimation of Spawning Fish to Low Salinity

On 20 October 1971 it was discovered that only 4 of the 26 fish acclimated to 15‰ seawater were females, whereas 15 of the 26 fish at 33‰ were females. The random assignment of fish to the two tanks had somehow resulted in a great disparity in their sex ratios. Two of the four female fish from 15‰ biopsied on 20 October 1971 had well-developed ovaries, showing that gonadal maturation can take place in a salinity of 15‰. The two well-developed females, as well as one of the poorly developed ones, were spawned with hormone injections; the oocyte size-frequency distributions from biopsies of the three fish shortly before injection are shown in Figure 14.

TABLE 8.—Multiple regression equations for percentage fertilization, total hatch, and viable hatch, as functions of temperature and salinity. Y = arcsin (percentage)$^{1/2}$, X_1 = temperature (C), X_2 = salinity (‰).

Fertilization		
Series A:	Y =	$-3.89030 + 0.25964X_1 + 0.10770X_2 - 0.00476X_1^2 - 0.00125X_2^2 - 0.00128X_1X_2$
Series B:	Y =	$-2.76156 + 0.14033X_1 + 0.12125X_2 - 0.00240X_1^2 - 0.00149X_2^2 - 0.00055X_1X_2$
Total hatch		
Series A:	Y =	$-8.55800 + 0.72293X_1 + 0.04177X_2 - 0.01482X_1^2 - 0.00073X_2^2 - 0.00014X_1X_2$
Series B:	Y =	$-13.40397 + 1.06566X_1 + 0.10817X_2 - 0.02115X_1^2 - 0.00157X_2^2 - 0.00070X_1X_2$
Viable hatch		
Series A:	Y =	$-3.91134 + 0.31755X_1 + 0.02932X_2 - 0.00645X_1^2 - 0.00046X_2^2 - 0.00017X_1X_2$
Series B:	Y =	$-9.99277 + 0.81039X_1 + 0.07829X_2 - 0.01620X_1^2 - 0.00117X_2^2 - 0.00066X_1X_2$

order equations are useful in that they allow computation of optimal conditions (Box 1956). The resulting values (Table 9) show a thermal optimum at about 24°C for total and viable hatch in both series, and optima of 23° and 25°C for fertilization in Series A and Series B, respectively. The calculated salinity optimum for fertilization was considerably higher in Series B than in Series A (36 vs. 31‰), but in both series the optimal salinities for hatching were below those for fertilization, ranging from 26 to 29‰. The optimal responses estimated at these points from the equations (Table 9) are below the maximal values actually recorded (cf. Tables 2 and 7), another indication of the lack of fit of the second order polynomial. The calculated positions of the optima, however, are the best available estimates of the true optima. These experiments were designed primarily to cover wide ranges of the two factors under consideration, and the arrangement of treatments unfortunately does not allow testing of the

TABLE 9.—Optimum temperatures and salinities for fertilization, total hatch, and viable hatch, estimated from the regression equations (Table 8). Also listed are the optimum percentage fertilization, total hatch, and viable hatch, calculated from the regression equations at the estimated temperature and salinity optima.

Item	Temperature (°C)	Salinity (‰)	Percentage
Fertilization:			
Series A	23.1	31.3	50.3
Series B	25.1	36.1	85.5
Total hatch:			
Series A	24.3	26.3	47.6
Series B	24.7	28.9	94.3
Viable hatch:			
Series A	24.3	27.4	11.2
Series B	24.5	26.6	67.3

The freezing point depression of blood serum from fish acclimated to 15‰, determined by the melting point method of Gross (1954), was 0.64 ± 0.066°C (mean ± SD, n = 12 fish), and that of fish from 33‰ was 0.63 ± 0.076°C (n = 12 fish). The two groups did not differ significantly, nor was

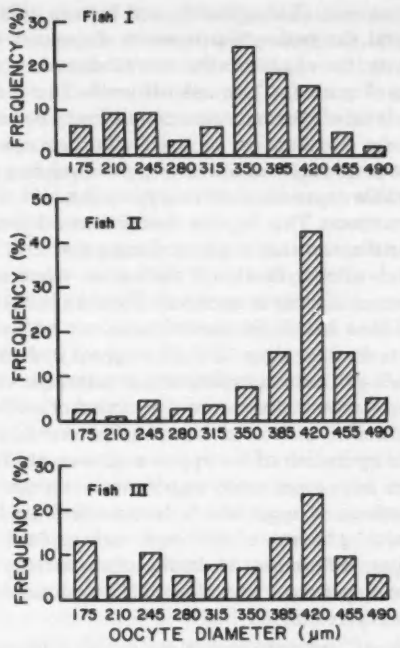

FIGURE 14.—Oocyte size-frequency distributions, based on ovarian biopsies, from fish acclimated to 15‰.

TABLE 10.—Fertilization success for eggs obtained from fish acclimated to 15‰.

Salinity (‰)	Percentage fertilization		
	Fish I	Fish II	Fish III
10	0	0	0
15	19.7	73.8	42.2
20	24.2	86.8	53.4
30	2.5	31.1	88.5
40	0.9	18.7	79.2
45	0	21.2	85.3
50	0	20.4	63.3

TABLE 11.—Percentage total and viable hatch of fertilized eggs at various salinities for eggs from fish acclimated to 15‰. For each fish, there were two replicate groups of eggs at each salinity.

Salinity (‰)	Fish I		Fish II		Fish III	
	a	b	a	b	a	b
			Total hatch			
15	23.4	22.0	87.1	79.8	97.0	92.6
20	30.5	44.2	86.7	86.3	97.0	95.7
30	10.9	2.0	46.9	66.0	97.9	94.9
40	—	—	80.0	80.9	84.8	68.8
45	—	—	71.2	71.4	65.7	76.3
50	—	—	35.9	31.0	22.8	45.8
			Viable hatch			
15	17.0	20.0	66.3	50.5	79.2	72.6
20	27.1	26.9	62.7	70.3	82.7	76.5
30	8.7	0	37.5	49.2	84.3	79.9
40	—	—	43.0	56.1	55.3	44.7
45	—	—	18.1	12.6	19.4	22.9
50	—	—	0	0	0	0

there a significant difference between sexes within each group (Mann-Whitney *U* test; Siegel 1956).

The fish with poorly developed ovaries (Fish I) became listless and swam in a disoriented manner after the hormone injection; 5 days after spawning, it still spent most of its time resting on its side on the bottom of the tank. At this point the fish was sacrificed and dissected, revealing some large, hydrated eggs with coalesced yolk, 665-735 μm in diameter, along with many unhydrated eggs still in their follicles, measuring 350 μm in diameter. Eggs obtained from the hormone-induced spawning of this fish showed low fertility, significant numbers being fertilized only at 15 and 20‰, with a maximum of 24.2% fertilized at 20‰ (Table 10). The hatching success of fertilized eggs was also poor, with a maximum total hatch of 44.2% at 20‰ (Table 11). A few embryos and larvae produced by this fish displayed various degrees of cyclopia, a deformity rarely seen in other batches of eggs.

As expected, the two ripe fish produced much better eggs, with maximum fertilization percentages of almost 90% (Table 10). Eggs from Fish II had a lower optimum salinity than those from Fish III and were more sensitive to high salinities (Table 10). No fertilization took place at 10‰, as was the case with eggs from fish living at 33‰.

Hatching at 15, 20, and 30‰ was better in eggs from Fish III than in those from Fish II, despite the better fertilization success of the latter at 15 and 20‰ (Table 11). Hatching at 40, 45, and 50‰ was comparable in the two batches of eggs. Eggs from Fish II hatched more successfully at 15 and 20‰ than at 30‰, whereas those from Fish III hatched equally well at 15, 20, and 30‰. The incidence of postmature unhatched eggs was similar to that in eggs from Series A and Series B, with most appearing at 15 and 20‰, few at 30‰, and very few or none above 30‰.

The hatching success at various salinities (20, 30, 40, and 50‰) of the best batch of eggs from fish living at 15‰ (i.e., from Fish III) was compared with that of the best batch of eggs from fish at 33‰ (Series B) at the same temperature (24°C) and salinities, by ANOVA (an arcsin-square root transformation was applied to the percentages).

Neither total nor viable hatching success differed significantly between the two groups. Therefore, acclimation of spawning fish to a low salinity did not affect the salinity tolerance of the eggs in any detectable way. Effects of acclimation salinity on egg size and buoyancy will be discussed elsewhere (May in preparation).

DISCUSSION

Fertilization and early development in *Bairdiella icistia* are stenothermal and stenohaline processes. The approximate limits for successful development, from fertilization to yolk exhaustion, are 20° to 28°C and 15 to 40‰, although a certain interaction of the two factors is apparent, development being more successful at the higher salinities when the temperature is relatively low, and at the higher temperatures when the salinity is relatively low. The limits within which successful reproduction can take place are defined by the most sensitive stages and events in development. The lower limit of salinity for bairdiella reproduction is defined by fertilization, since eggs cannot be fertilized at 10‰ or below, even though eggs fertilized at a higher salinity will develop at 10‰. However, the lowest salinity at which eggs remain buoyant may in some cases determine the lower salinity threshold for successful reproduction (May 1972). The upper salinity limit, and both the upper and the lower limits of temperature, are defined by the abilities of the embryos to develop. Fertilization is successful at 18°C but development is not; likewise, fertilization does take place at 30°C, and at salinities of 45‰ and above, but the hatching of viable larvae is greatly curtailed.

Fertilization in bairdiella is more limited by salinity than temperature over the ranges studied. The complete block to fertilization which occurs at 10‰ may be related to an inability of spermatozoa to function properly at this salinity. Although the egg itself seems to be unharmed by water of 10‰, at this salinity spermatozoa never attain the high intensity of activity that they do at higher salinities. At 15‰, where spermatozoan activity is more intense than at 10‰ but less intense than at higher salinities, fertilization occurs but is poorer than at higher salinities. Fairly high salinities seem to aid fertilization: the calculated optimum salinities for fertilization were higher than the optima for hatching in both Series A and Series B. It is possible that low calcium levels at low salinities inhibit the activity of spermatozoa (Yanagimachi and Kanoh 1953). In general, the greater the intensity of spermatozoan activity, the shorter is the overall duration of activity (Figure 3). Thus a shortlived but extremely high level of spermatozoan activity may be necessary for fertilization in bairdiella, perhaps because penetration of the micropyle requires a considerable expenditure of energy on the part of the spermatozoa. This implies that the actual process of fertilization takes place during the first few seconds after hydration of the sperm, when spermatozoan activity is maximal. Haydock (1971) reports that bairdiella spermatozoa are no longer able to fertilize eggs 30 s after sperm hydration. In such a situation, experimental technique could have a marked influence on the success of artificial fertilization, since a delay of a few seconds between hydration of the sperm and contact of the sperm with eggs could significantly reduce the percentage of eggs which become fertilized. A technical problem of this sort may explain the puzzling differences in fertilization success between eggs from Fishes II and III, acclimated to 15‰ (Table 10).

Several previous investigations of salinity effects on spermatozoan activity in other fishes provide interesting contrasts with the present results. Ellis and Jones (1939) found that spermatozoa of Atlantic salmon, *Salmo salar*, a fish which spawns in fresh water, were active for over 180 min in seawater diluted to 15 and 20% and that the duration of activity dropped off sharply above and below these salinities. Working with the longjaw mudsucker, *Gillichthys mirabilis*, Weisel (1948) observed that spermatozoa showed only feeble activity in seawater diluted to 17-24%, but activity was intense in 25% seawater and above; the duration of spermatozoan activity was maximal (over 50 h!) in 25% seawater and decreased at higher salinities, as it did in the case of bairdiella. Yamamoto (1951) found that spermatozoa of the flounder, *Limanda schrenki*, were active in normal seawater and in seawater diluted to 50%, but showed no activity (and no fertilizing capability) in 25% seawater. Hines and Yashouv (1971), on the contrary, found that mullet, *Mugil capito*, spermatozoa exhibited a gradual increase in duration of activity with increasing salinity up to the salinity of normal seawater, rather than a threshold. Dushkina (1973) reported that spermatozoa of Pacific herring, *Clupea harengus pallasi*, were most active at higher salinities (17-23‰), but remained active longest at the

lowest salinities (0.3-0.5‰), as was true for bairdiella; however, in herring the duration of spermatozoan activity was much longer (4-8 days at 6-7°C) and some fertilization occurred even in fresh water. Spermatozoan activity and its response to salinity appear to be extremely variable among fish species, which is hardly surprising in view of the diversity of habitats and modes of reproduction of fishes.

The large proportion of postmature unhatched eggs at low salinities (Table 6) reflects a high incidence of malformations under these conditions, the embryos being physically unable to break from the chorion. Edema seen among larvae in low salinities suggests that deformities and the inability to hatch may be related to osmotic problems. Battle (1929) noted a similar difficulty in hatching among embryos of fourbeard rockling, *Enchelyopus cimbrius*, in low salinities and attributed it to abnormally developed musculature, which prevented movements required to free the embryo from the egg case. An inability to complete hatching at low salinities has been reported for other species as well (Ford 1929; McMynn and Hoar 1953; Alderdice and Forrester 1967; Dushkina 1973). The generalization that gastrulation and hatching are the two developmental stages most sensitive to physical disturbance (e.g., Holliday 1969) seems valid in the case of bairdiella.

The finding that unfed bairdiella survive longest in low salinities and low temperatures is not unique. Nakai (1962) and Hempel and Blaxter (1963) likewise found that starving larvae of *Sardinops melanosticta* and *Clupea harengus* survived longer at lower salinities, and more rapid mortality among unfed larvae at higher temperatures has been observed on a number of occasions (e.g., Qasim 1959; Bishai 1960; Hempel and Blaxter 1963; Alderdice and Velsen 1971; Hamai et al. 1971). High temperatures increase metabolic rate, accelerate yolk absorption (May 1972), and no doubt hasten death from starvation. The effect of high salinities on larval physiology is less certain: a salinity effect on embryonic or larval oxygen consumption has not been demonstrated except after abrupt transfer (Holliday 1969), and salinity has only a small effect on the rate of yolk absorption in bairdiella (May 1972). High salinities may increase larval mortality by causing osmotic or ionic changes in the interior milieu, although the larvae of some species have proved capable of osmoregulating over rather wide ranges of salinities (Holliday 1969). Lower levels of activity have been observed among larvae of some species in low salinities (Hempel and Blaxter 1963; Holliday 1965), and may reduce their metabolic demand and thus extend their survival time (Holliday 1965).

The salinity tolerance of bairdiella eggs is not significantly affected by acclimation of the parent fish to low salinity (15‰). This might suggest that the enhanced survival at low salinities which Solemdal (1967) observed in eggs from the Finnish population of flounder, *Pleuronectes flesus*, has a genetic basis. If acclimation of spawning fish to low salinities does not cause an increase in embryonic tolerance to low salinities, one might expect that high-salinity acclimation would be similarly ineffectual in aiding embryonic survival at high salinities. This supposition should be verified experimentally; but, if valid, it implies that salinity responses determined on eggs from fish living in ordinary seawater should be accurate predictors of reactions to different salinities in nature, except where genetic adaptation has occurred. This could be a significant advantage in cases where it is important to estimate the effects of rising salinities in specified habitats, such as the Salton Sea or the Gulf of California, where high salinities may in the future pose a threat to existing stocks of fish.

Because of the unusual chemical nature of the Salton Sea, it is impossible to estimate the salinity tolerance of bairdiella eggs in Salton Sea water from the present data concerning their responses in ordinary seawater. There is evidence that the ionic composition of Salton Sea water has a deleterious effect on the survival of eggs and larvae (Lasker et al. 1972; May 1972), so that the upper salinity limits defined in the present study are probably higher than those which hold for bairdiella in the Salton Sea.

The spawning season of bairdiella occurs during a period of rapidly rising temperatures. In the Salton Sea this species spawns mainly in April and May, with a peak of spawning probably in mid-May (Whitney 1961; Haydock 1971). Maximum surface temperatures in the Salton Sea are plotted in Figure 15, where the spawning time of bairdiella is also shown. It is clear that some bairdiella may spawn in water of 30°C or higher, although most spawning is probably finished before temperatures reach this level. Whitney (1961) reports finding bairdiella eggs in 1955 as late as 1 August, which means they could have been exposed to the undoubtedly lethal temperature of

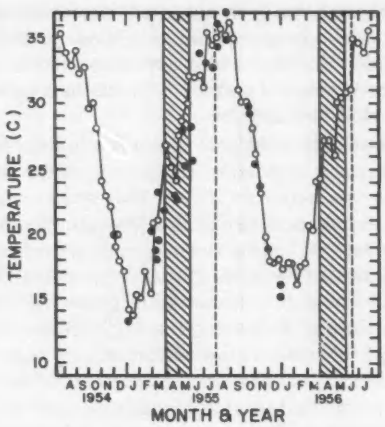

FIGURE 15.—Maximum surface temperatures in the Salton Sea. Open circles: measurements made at Sandy Beach, Salton Sea, from August 1954 to July 1956 (after Carpelan 1961). Closed circles: measurements made at various stations on the Salton Sea during 1967 (after Young 1970). The shaded areas indicate the major spawning period of *Bairdiella icistia*, and the vertical dotted lines indicate the latest records of bairdiella eggs in the plankton in 1955 and 1956, according to Whitney (1961).

35°C. Such late spawning by bairdiella seems unlikely, however, and Whitney may have collected eggs of the orangemouth corvina, *Cynoscion xanthulus*, which spawns during the summer and probably produces similar eggs, rather than bairdiella. In any event, it seems possible that late spawning bairdiella in the Salton Sea could release their eggs in water with a temperature high enough to reduce embryonic and larval survival severely. In view of the temperature-salinity interaction which occurs in the case of both embryonic and larval tolerance, bairdiella which spawn at relatively low temperatures early in the season will probably have a selective advantage as the salinity of the Salton Sea rises.

In the absence of detailed information on the distribution of bairdiella and the physical conditions obtaining in its native habitat, the Gulf of California, it is difficult to apply the present findings to the ecology of this species in that area. However, the utilization of Colorado River water for irrigation has caused an increase in the river's salinity (Wolman 1971); if this, and the accompanying reduced flow of fresh water into the upper Gulf of California, results in a significant rise in salinity in areas where bairdiella spawn, the combined action of salinity stress and heat in this arid region could adversely affect early survival in the local bairdiella population. The warm brine effluent from a proposed desalination plant in this area (Thomson et al. 1969) could aggravate the situation considerably if dispersal of the effluent is not adequate.

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FITTING THE GENERALIZED STOCK PRODUCTION MODEL BY LEAST-SQUARES AND EQUILIBRIUM APPROXIMATION[1]

WILLIAM W. FOX, JR.[2]

ABSTRACT

A least-squares method for fitting the generalized stock production to fishery catch and fishing effort data which utilizes the equilibrium approximation approach is described. A weighting procedure for providing improved estimates of equilibrium fishing effort and an estimator of the catchability coefficient are developed. A computer program PRODFIT for performing the calculations is presented. The utility and performance of PRODFIT is illustrated with data from a simulated pandalid shrimp population.

The production model approach to fish stock assessment is simply an adaptation of the Lotka-Volterra population equations into the situation of a population exploited by man. The earliest such adaptation was by Graham (1935) in assessing the potential production from North Sea fish stocks. The major development of this approach in fisheries management, though, is due to Schaefer (1954, 1957) who initiated it as a management tool for the yellowfin tuna fishery of the eastern tropical Pacific Ocean. While there has been an attempt at a detailed extention of the production model approach to multispecies fisheries (Lord 1971), the usual application has been on a single species stock.

Mathematical formulation of the production model begins with the general differential equation

$$dP/dt = P_t g(P_t) - P_t h(f_t) \quad (1)$$

where P_t is the population size at time t, $P_t g(P_t)$ is the population production function encompassing the effects of reproduction and natural mortality (and growth in weight if biomass is the population unit), and $h(f_t)$ is the fishing mortality coefficient exerted by f_t units of fishing effort. Fishing effort is assumed to be standardized from nominal fishing effort such that $qf_t = F_t$, where F_t is the instantaneous coefficient of fishing mortality and q is a constant (the catchability coefficient), giving $qf_tP_t = dC/dt$, the rate of catch. At equilibrium, that is $dP/dt = 0$, the catch rate equals the production rate such that an equilibrium yield, Y, is obtained

$$Y = qfP = Pg(P). \quad (2)$$

The most general assumptions about the form of $P_t g(P_t)$ are that it should 1) approach zero as P_t approaches some environmental capacity, P_{max}, and 2) increase to some maximum at a population size smaller than the environmentally limited size. Practically, the function should be simple, since in any case the approach is a gross simplification of population dynamics. The most flexible, simple function advanced for $P_t g(P_t)$ is a simple case of Bernoulli's equation (Chapman 1967; Pella and Tomlinson 1969)

$$P_t g(P_t) = HP_t^m - KP_t \quad (3)$$

where H, K, and m are constant parameters.[3] Equation (3) includes the logistic function when $m = 2$ (Schaefer 1954, 1957) and the Gompertz function $[K'P_t - H'P_t \ln P_t]$ as $m \rightarrow 1$ (Fox 1970). Equation (3), hereafter referred to as the generalized stock production model after Pella and Tomlinson (1969), approaches zero at $P_{max} = (K/H)^{1/(m-1)}$ and has a maximum $P_{opt} = [m^{1/(1-m)}] \cdot P_{max}$.

Three equilibrium relationships can be derived by the substitution of Equation (3) in Equation (2) to obtain

1) Yield and population size

$$Y = HP^m - KP, \quad (4)$$

2) Population size and fishing effort

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[3]When formulated as in Equation (3), H and K are positive for $m < 1$, but are negative for $m > 1$.

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$$P = \left(\frac{K}{H} + \frac{q}{H} f\right)^{\frac{1}{m-1}} \quad (5)$$

3) Yield and fishing effort

$$Y = f\left(\frac{Kq^{m-1}}{H} + \frac{q^m}{H} f\right)^{\frac{1}{m-1}} \quad (6)$$

The critical points, useful as management implications and previously derived by Pella and Tomlinson (1969), are:

$$f_{opt} = K\left(\frac{1}{m} - 1\right)/q \quad (7)$$

$$P_{opt} = [K/(mH)]^{\frac{1}{m-1}} \quad (8)$$

and

$$Y_{max} = H[K/(mH)]^{\frac{m}{m-1}} - [K^m/(mH)]^{\frac{1}{m-1}}, \quad (9)$$

where f_{opt} is the amount of fishing effort required to produce Y_{max}, the maximum sustainable average yield (MSAY),[4] and P_{opt} is the equilibrium population size obtained at f_{opt}. Figure 1 demonstrates the flexibility of the generalized stock production model with three values for m (0.5, 2.0, 4.0); each curve has the same value for P_{max} and Y_{max}.

In utilizing the production model for analysis of the status of a particular population, the usual basic assumptions are that 1) the model is being applied to a closed single unit population, 2) the concept of equilibrium conditions[5] applies to the population under analysis, and 3) the age-groups being fished have remained, and will continue to remain, the same. If one is able to obtain data which represent equilibrium conditions at three or more population levels, then no additional assumptions are needed to fit the production model. In most fishery data sets, however, no real period of equilibrium conditions will exist. Using data from the transitional states of a population requires the additional assumptions that both 1) time lags in processes associated with population change and 2) deviations from the stable age structure at any population level have negligible effects on the production rate, $P_t g\ (P)_t$ (Schaefer and Beverton 1963).

Schaefer (1954, 1957) pioneered the use of transitional state data for fitting a production model (the logistic form) to catch and fishing effort data. Schaefer's (1957) method for estimating the parameters consisted of approximating differential equation (1) with two finite difference equations and then iteratively solving them. Pella and Tomlinson (1969) greatly improved upon Schaefer's method by demonstrating that a catch history of a fishery could be predicted from the fishing effort history, initial estimates of the production model parameters, and the integrated form of Equation (1). Then final parameter estimates could be obtained by a pattern search routine which finds those parameters which minimize the residual sum of squared differences between

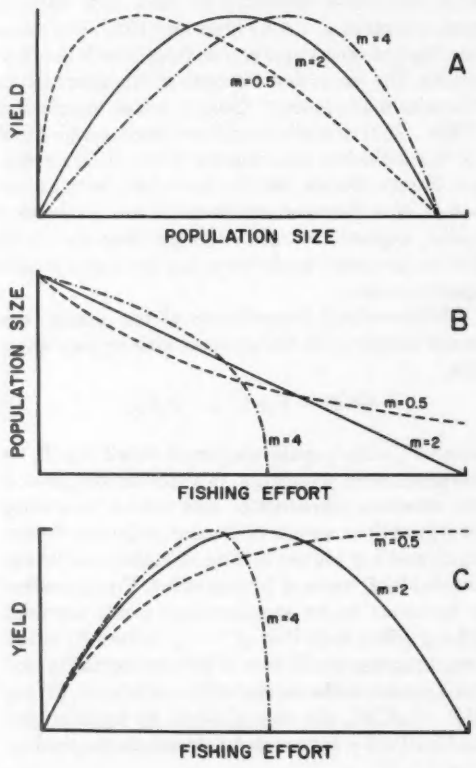

FIGURE 1.—Equilibrium relationships of the generalized stock production model for three values of m. (A) Equilibrium yield and population size; (B) population size and fishing effort; (C) equilibrium yield and fishing effort.

[4] Y_{max} is usually referred to as the maximum sustainable yield (MSY). The term MSY, however, does not convey that in reality the yield will fluctuate due to changes in the population even if the fishing effort and catchability coefficient remain constant. Hence, the "equilibrium yield" curve represents a curve of yield that is sustainable at some average level.

[5] The definition of equilibrium adopted here, essentially that of Beverton and Holt (1957), is: given a constant rate of fishing, including zero, a population will achieve a state where, on the average, it will not change in size or characteristics.

the observed and predicted catches. While these two estimation methods are very different in their degree of sophistication, they are fundamentally the same in that both methods utilize the prediction of population transitional state changes by the production model. For convenience, this approach will be subsequently referred to as the transition prediction approach.

Gulland (1961) established a second approach to fitting production models with transitional state data. Gulland's approach estimates the level of fishing effort which, if equilibrium obtained, would produce, on the average, the observed level of catch per unit effort in each year of the fishery. Then the set of paired catches per unit effort and estimated equilibrium fishing effort units are fitted to one of the equilibrium relationships given by, or derived from, Equation (4), (5), or (6). This approach will be referred to subsequently as the equilibrium approximation approach.

Clearly, the transition prediction and equilibrium approximation approaches are basically different. The transition prediction approach is obviously intimately based upon the transition state population assumptions. On the other hand, the degree to which the equilibrium approximation approach is dependent on these assumptions is unclear. This paper presents a least-squares method and a computer program PRODFIT, which uses the equilibrium approximation approach to estimate the parameters (and indices of their variability) of the generalized stock production model. A weighting procedure for providing improved estimates of equilibrium fishing effort and an estimator of the catchability coefficient are developed. The utility and performance of computer program PRODFIT is illustrated by fitting deterministic and stochastic data from a simulated pandalid shrimp population. Some cursory comparisons between the equilibrium approximation and transition prediction approaches are made by repeating the pandalid shrimp simulated data fits with GENPROD, the computer program written by Pella and Tomlinson (1969).

FITTING METHOD

The equilibrium approximation approach was first outlined in Gulland (1961), but is more fully explained in Gulland (1969:120). Gulland's method involves relating the annual catch per unit effort in year i, U_i, to the fishing effort averaged over some number of years, T. Gulland (1961) first defined T as the mean life expectancy of an individual in the fishable population, or Z^{-1}, where Z is the instantaneous total mortality coefficient and the value of Z^{-1} is rounded off to the nearest integer. Subsequently, Gulland (1969) defined T as the average fishable duration of a year class (again to the nearest whole year)—he provided the following example: if recruitment is at 4 yr and if most of the catch in year i consists of 4 to 9 yr-old fish, then the average fishable duration is about 3 yr so U_i would be related to an average of f_i, f_{i-1} and f_{i-2}. The general formulation for the averaged fishing effort in year i is

$$\bar{f}_i = \frac{1}{T} \sum_{j=i-T+1}^{i} f_j \tag{7}$$

A discussion of the rationale for, and performance of, Gulland's averaging method is given by Gulland (1969:120).

Weighted Average Fishing Effort Method

In this paper a different tack is taken which results in approximating equilibrium fishing effort with a weighted average. The catch per unit effort of the incoming year class j in year i, U_{ij}, is related to the amount of effort in year i; that of the previous year class, $U_{i,j-1}$, is related to the fishing effort in years i and $i-1$; that of the year class which entered 2 yr previously, $U_{i,j-2}$, is related to the fishing effort in years i, $i-1$, and $i-2$; and so forth. The catch per unit effort of the total fishable population, assuming equal catchability, is

$$U_i = U_{i,j} + U_{i,j-1} + U_{i,j-2} + \cdots + U_{i,j-k+1}$$

for k year classes. For the simplest case where the incoming year class is recruited at the beginning of each year's fishing season, therefore,

$$U_i \sim \{k \cdot f_i + (k-1) \cdot f_{i-1} + \cdots + f_{i-k+1}\}. \tag{8}$$

Equation (8) suggests a weighted average of fishing effort over the total number of years that a year class contributes significantly to the fishery, or

$$\bar{f}_i = \{k \cdot f_i + (k-1) \cdot f_{i-1} + \cdots + f_{i-k+1}\} / \{k + (k-1) + \cdots + 1\}. \tag{9}$$

An arithmetic average rather than a geometric average is suggested because most applications are on catch in weight, i.e. while year classes decline exponentially in terms of numbers they concomitantly increase in terms of mean weight per individual.

The weighting procedure can be more precise if it is known when during the year of record that recruitment occurs. For example, if recruitment occurs at midseason during the year of record for a fishable population of three year classes, $\bar{f}_i$ changes from $\left\{3f_i + 2f_{i-1} + f_{i-2}\right\}$ /6 to $\left\{2.5f_i + 1.5f_{i-1} + 0.5f_{i-2}\right\}$ /4.5. Further precision is gained if k is varied from year to year with the level of fishing effort, since at high fishing rates fewer year classes will contribute significantly to the catch than at low fishing rates. Further adjustments can be made for unequal catchability among the year classes.

The unweighted method of averaging the fishing effort, Equation (7), and the new weighted method, Equation (9), will be compared in a subsequent section of this paper.

Estimation Procedure

Gulland (pers. commun.)[6] prefers an eye-fitted curve for estimating the equilibrium relationship between U_i and f_i because of the oversimplification of the method and the errors associated with usual catch and effort data. However, these reasons should not defer the seeking of a more precise method of fitting a curve nor the taking advantage of error estimation schemes, if the simplifications and assumptions are kept in mind. On the contrary, it will be demonstrated that, at least for some controlled conditions, the equilibrium approximation approach provides reasonably good results.

Equation (5) may be written in terms of catch per unit effort and averaged fishing effort as

$$U_i = [(Kq^{m-1}/H) + (q^m/H)\bar{f}_i]^{1/(m-1)} \quad (10)$$

or simply

$$U_i = (\alpha + \beta \bar{f}_i)^{1/(m-1)}. \quad (11)$$

Equation (11) is a nonlinear function with three parameters which does not require simultaneous estimation of the catchability coefficient, q. The critical points in terms of the parameters of Equation (11) are

$$f_{opt} = (\alpha - \alpha m)/(m\beta) \quad (12)$$

$$U_{opt} = (\alpha/m)^{1/(m-1)} \quad (13)$$

and

$$Y_{max} = \frac{(\alpha - \alpha m)(\alpha/m)^{1/(m-1)}}{m\beta}. \quad (14)$$

Given the data set $\left\{U_i, \bar{f}_i\right\}$, where $i = 1...n$ observations, the least-squares criterion for estimating the parameters α, β, and m is to minimize the function

$$S = \sum_{i=1}^{n} W_i(U_i - \hat{U}_i)^2 \quad (15)$$

where the W_i are statistical weights, and $\hat{U}_i$ are the predicted equilibrium catches per unit effort from Equation (11). The statistical weights,

$$W_i = (\hat{U}_i)^{-2}, \quad (16)$$

are derived from the assumption of the multiplicative error structure as suggested by Fox (1971). Weighting as in Equation (16) will usually give the greatest weight to observations at the highest level of averaged fishing effort; in many cases these also will be the most recent observations. Giving greater weight to observations at high effort levels will tend to give the greatest weight to observations with the greatest temporal and spatial coverage of the population. In addition, giving the greatest weight to the most recent data is especially advantageous when approaching the Y_{max} level during a period increasing fishing effort because the observations nearest the Y_{max} level receive the greatest weight.

Up to now no mention has been made on the estimation of the catchability coefficient, q. This is because experience with GENPROD and stochastic simulation studies have indicated that poor results are frequently obtained from the simultaneous estimation of q (Pella and Tomlinson 1969; Fox 1971). Once that α, β, and m have been estimated, q may be treated as a conditional probabilistic variable and estimated as a mean value. Two tacks were selected, the difference method and the integral method.

[6]John A. Gulland, Food and Agricultural Organization, Rome, Italy.

The difference method involves writing Equation (1) as a finite difference equation for the production model in terms of catch per unit effort and the estimates for α, β, and m as

$$\frac{1}{q}\frac{\Delta U_i}{\Delta t} = \frac{1}{\hat{\beta}} U_i^{\hat{m}} - \frac{\hat{\alpha}}{\hat{\beta}} U_i - f_i U_i \qquad (17)$$

for each year i; Δt is taken as one unit, Equation (17) is divided through by U_i, summed over the $n - 2$ yr that ΔU_i can be estimated, and then solved for $\hat{q}_S$,

$$\hat{q}_S = \left[\sum_{i=2}^{n-1} \frac{\Delta \hat{U}_i}{U_i}\right] / \left[\frac{1}{\hat{\beta}} \sum_{i=2}^{n-1} U_i^{\hat{m}-1} - (n-2)\frac{\hat{\alpha}}{\hat{\beta}} - \sum_{i=2}^{n-1} f_i\right] \qquad (18)$$

where

$$\Delta \hat{U}_i = (U_{i+1} - U_{i-1})/2. \qquad (19)$$

This method has provided reasonable estimates with the logistic ($m = 2$) and Gompertz ($m \to 1$) forms of the production model for several fisheries (Fox 1970).

Pella and Tomlinson (1969) observed that Equation (19) can be a poor estimator of the change in stock size during year i under certain circumstances. The integral method avoids this problem by writing Equation (17) as a differential equation

$$\frac{dU}{U\left(-\frac{\hat{\alpha}}{\hat{\beta}} - f^* + \frac{1}{\hat{\beta}} U^{\hat{m}-1}\right)} = q\,dt, \qquad (20)$$

where f^*, the effective effort having been exerted between years i and $i+1$, is estimated by

$$\hat{f}^* = (f_i + f_{i+1})/2. \qquad (21)$$

The integral of Equation (20) after rearranging some terms is

$$\hat{q}_I = \ln\left[\left|\left(zU_i^{1-\hat{m}} + \frac{1}{\hat{\beta}}\right)/\left(zU_{i+1}^{1-\hat{m}} + \frac{1}{\hat{\beta}}\right)\right|\right]/(z\hat{m} - z) \qquad (22)$$

where

$$z = -\hat{\alpha}/\hat{\beta} - \hat{f}^*.$$

The fact that Equation (22), as an estimator of q, gives negative values when the stock changes in one direction, depending on whether m is greater or less than 1, is remedied by taking the absolute value of q. Also, since q is constrained against being less than zero, the geometric mean will probably be a better estimator than the arithmetic mean (this will be demonstrated to be so in at least one case), such that

$$\hat{q}_I = e^{\sum_{i=1}^{n-1} \ln|\hat{q}_i|/(n-1)} \qquad (23)$$

becomes the integral estimator.

Variability Measures

Some measure of the variability of the parameter estimates can be made using the "delta" method (Deming 1943). If S is the weighted residual sum of squares for the final parameter estimates, a variability index matrix, V, is computed by

$$V = (X'WX)^{-1} S/(n-3) \qquad (24)$$

where W is an n by n diagonal matrix of the statistical weights, X is an n by 3-parameter matrix of first partial derivatives of Equation (11) with respect to each parameter (given in the Appendix). The diagonal elements of V are variability indices of the parameter estimates and the off-diagonal elements of V are covariability indices. Since Equation (11) is nonlinear, the independent variable is not without error, the errors in the dependent variable are correlated, and the statistical weights are random variables, it is virtually impossible to make probability statements about the accuracy of the parameter estimates (Draper and Smith 1966). However, V gives some index of the variability inherent in the data which is useful largely for comparative purposes between different fisheries and data sets. For convenience, an error index may be formulated as

$$E_x = [100\sqrt{V(\hat{x})}]/\hat{x} \qquad (25)$$

where $\hat{x}$ is the estimated parameter and $V(\hat{x})$ is its corresponding variability index. Variability and error indices of Y_{max}, f_{opt}, and U_{opt} also may be computed by the "delta" method (see Appendix) and the elements of V (Equation 24).

Program PRODFIT

A computer program PRODFIT, in FORTRAN IV language, was written to perform the calculations described above. A brief description of the program's options and mode of operation is given below.

DATA INPUT OPTION. *Option 1.*—A catch

and fishing effort history, $\{C_i, f_i\}$, of $i = 1 \ldots n$ years length and a vector of significant year class numbers $\{k_i\}$ are read in. There may be embedded zeros, if they are true zeros and do not simply reflect a lack of information. The only real problem with unreal zeros, however, occurs in the estimation of q. The catch per unit effort vector is computed internally and the averaged fishing effort vector is computed by Equation (9) with SUBROUTINE AVEFF.

Option 2.—If one wishes to compute the averaged fishing effort vector by another method or if data are obtained which represent equilibrium conditions, then this option is selected and the vectors of catch per unit effort and averaged (or equilibrium) fishing effort $\{U_i, \bar{f}_i\}$ are read in directly. No estimate of q can be made, however.

STARTING VALUES OPTION. *Option 1*.—Initial estimates of the parameters are computed in SUBROUTINE INEST and the user provides the starting estimate for m, either 0, 1, or 2. *Option 2*.—Occasionally the data are so variable that INEST does not provide compatible starting values for the parameters. In this case, or in any case, the user may opt to enter directly all the initial parameter estimates.

MODEL OPTION. The user may allow PRODFIT to estimate m to any desired precision. Frequently, however, the data are so variable that no significant reduction in the residual sum of squares is obtained by varying m. The user then has the option to fix m at 2, the logistic model (Schaefer 1957); at 1, the Gompertz model (Fox 1970); or at 0, the asymptotic yield model.

WEIGHTING OPTION. The user may select the statistical weights as Equation (16) or may choose to not weight the observations, i.e., $W_i = 1$ for all i.

CATCHABILITY COEFFICIENT. The catchability coefficient, q, is estimated by Equation (22), but both the geometric and arithmetic averages are computed.

Program PRODFIT uses an adaptation of the same pattern search optimization routine, MIN, as contained in GENPROD (Pella and Tomlinson 1969) to locate the least-squares parameter estimates. A more sophisticated Taylor series approach (Draper and Smith 1966) was attempted initially, but severe distortion of the sum-of-squares space prevented reasonable convergence. In order to facilitate termination of the searching procedure, the sum-of-squares space is searched with m and a transformation of the parameters α and β to

$$U_{max} = \alpha^{1/(m-1)} \tag{26}$$

$$Y_{max} = \frac{(\alpha - \alpha m)(\alpha/m)^{1/(m-1)}}{m\beta} \tag{27}$$

where U_{max} is the unexploited population size in terms of catch per unit effort. Neither U_{max} nor Y_{max} change greatly with moderate changes in m.

The output of PRODFIT provides a listing of the input data, the transformed data, initial parameter estimates, the iterative solution steps, the final estimates of α, β, and m and their variability indices, the management implications of the final model U_{max}, U_{opt}, f_{opt}, and Y_{max} and their variability indices, the observed and predicted values and error terms, and estimates of the catchability coefficient, q.

A listing of program PRODFIT and a user's guide are available on request from the author.

COMPARATIVE EXAMPLES OF THE EQUILIBRIUM APPROXIMATION METHODS

Two methods of averaging fishing effort which attempt to approximate equilibrium conditions have been presented, the unweighted method (Equation 7) and the new weighted method (Equation 9). In order to compare these two methods, catch histories for a simulated pandalid shrimp fishery (Fox 1972) were generated using a generalized exploited population simulation model GXPOPS (Fox 1973). It should be noted, however, that the comparisons are, for the most part, simply illustrative. It is virtually impossible to demonstrate conclusively which is the better method because there is an infinite choice of life histories, parameter values, fishing effort histories, and stochastic variation representations.

Equilibrium values for the unexploited population biomass in terms of catch per unit effort (U_{max}), the maximum equilibrium yield (Y_{max}), and optimum fishing effort (f_{opt}), were determined empirically by running the simulation model

(Table 1). The catchability coefficient, q, was assumed to be 1.0. Figure 2 presents the equilibrium values of catch per unit effort and yield at fishing effort values ranging from 0.0 to 1.3 for the simulated shrimp population. Above $f = 1.3$ the population level did not stabilize in 25 yr of simulation and at $f = 2.0$ the population was definitely extinguished. The equilibrium data for $f = 0.0$ to 1.3 were fit to the generalized stock production model with PRODFIT to illustrate the obtainable degree of correspondence. The generalized stock production model very closely approximates the equilibrium values for the simulated pandalid shrimp population being slightly low in the range of $f = 0.7$ to 1.1 and slightly high beyond $f = 1.1$ (Figure 2). The estimated parameters are also very close (Table 1).

TABLE 1.—Empirical management implications for the simulated pandalid shrimp population and those estimated for the generalized stock production model with PRODFIT.

Method	Y_{max}	U_{max}	f_{opt}	q	m
Empirical	5.60	17.96	1.02	1.0	—
PRODFIT	5.56	17.91	1.11	—	0.604

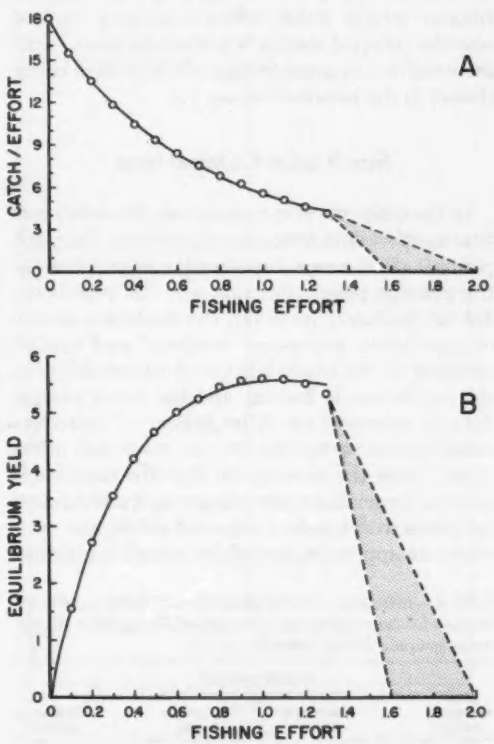

FIGURE 2.—Fit of the generalized stock production model (line) to simulated equilibrium values (circles) of (A) catch per unit effort and (B) yield by computer program PRODFIT. Shaded areas represent nonequilibrium.

The problem which confronts a fishery scientist is to estimate the parameters of Table 1, hence the equilibrium relationship of Figure 2, from catch and fishing effort data representing transitional rather than equilibrium states. To illustrate the efficacy of the equilibrium approximation approach and to provide a comparison between the two fishing effort averaging methods, a 12-yr fishing effort history was selected which approximates the rapid expansion of fishing for *Pandalus borealis* in Ugak Bay, Alaska. Exploiting the simulated shrimp population with the fishing effort history produced the catch and catch per unit effort history in Figure 3. Two comparisons were made, the first using the deterministic data shown in Figure 3 and the second introducing some random error.

Deterministic Comparison

The appropriate averaging time, k, for the weighted average method is four since the fishable part of the simulated shrimp population consists of four significant year classes. The appropriate averaging time, T, for the unweighted average method is 2 since the average duration of the fishable phase is 2 yr. The results of fitting the

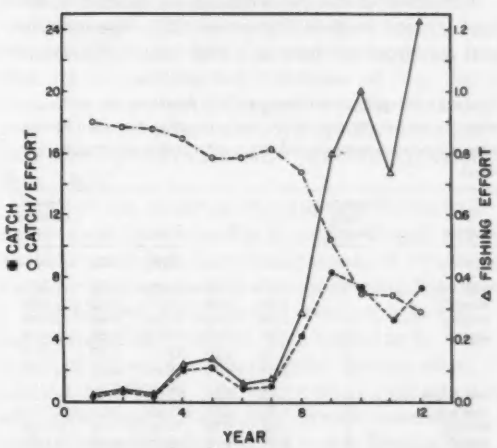

FIGURE 3.—Catch (dots) and catch per unit effort (circles) calculated with a fishing effort history (triangles) from the simulated pandalid shrimp population.

12-yr catch and fishing effort history by both methods for a range of averaging times are given in Table 2. Examination of the appropriate row for each method in Table 2 clearly reveals that for this example the superior estimates were produced by the weighted average method. In fact, the maximum error among the weighted average estimates of m, Y_{max}, and U_{max} (the parameters used in searching for the least-squares solution) at $k = 4$ is only 1%.

The effect of different averaging times on the estimates of the parameters m, Y_{max}, and U_{max} is the same for both effort averaging methods. By increasing the averaging time, the estimates of m and Y_{max} decrease and the estimate of U_{max} increases. The residual sum of squares is minimum at the appropriate averaging time for the weighted method (i.e. at $k = 4$). For the unweighted method, however, the minimum residual sum of squares is at 1 yr greater than the appropriate criterion.

Another way of comparing the weighted and unweighted averaging methods is to examine how well they estimated the equilibrium fishing effort. The equilibrium fishing effort was computed for each year's observed catch per unit effort (Figure 3), using the production model fitted to the equilibrium data (Table 1) for interpolation. The estimated equilibrium fishing effort by the weighted average method was closest in 10 of the 12 yr and had a mean absolute error of less than one-third of the unweighted method (Table 3).

Estimates of the catchability coefficient, q, by the integral method, Equation (22), —geometric and arithmetic means—and the difference method, Equation (18), for the weighted ($k = 4$) and unweighted ($T = 2$) fishing effort averaging techniques are given in Table 4. The best estimator within either effort averaging method was the integral method's geometric mean, with the weighted average fishing effort method being closest to the assumed value, 1.0.

TABLE 2.—Empirical and estimated parameters for the simulated pandalid shrimp catch history using the equilibrium approximation approach and two methods of averaging fishing effort.

Method	Averaging time (k or T)	$\hat{m}$	$\hat{Y}_{max}$	$\hat{U}_{max}$	[1]$\hat{q}$	Mean squared error
Empirical	—	[2]0.60	5.60	17.96	1.00	—
Weighted average fishing effort[3]	1	1.16	7.26	17.63	0.42	1.3830
	2	1.35	6.48	17.61	0.62	0.3293
	3	0.86	6.02	17.82	0.86	0.0686
	[4]4	0.60	5.67	17.97	0.87	0.0500
	5	0.53	5.21	18.01	0.75	0.0913
	6	0.51	4.76	18.02	0.62	0.1236
Unweighted average fishing effort[5]	1	1.16	7.26	17.63	0.42	1.3830
	[4]2	1.09	6.17	17.69	0.70	0.1323
	3	0.35	6.10	18.07	1.12	0.0529
	4	0.28	5.36	18.14	0.69	0.2797

[1]Integral method, geometric mean.
[2]Estimated, Table 1.
[3]Equation (9); Program PRODFIT, unweighted estimates option.
[4]Appropriate averaging time.
[5]Equation (7); Program PRODFIT, unweighted estimates option.

TABLE 3.—Comparison of two estimates of equilibrium fishing effort for the simulated pandalid shrimp population catch history.

Year	Equilibrium effort[3]	Weighted average estimate[1] Effort	Weighted average estimate[1] Error	Unweighted average estimate[2] Effort	Unweighted average estimate[2] Error
1	0.0000	0.0000	−0.0000	0.0000	−0.0000
2	0.0072	0.0116	−0.0044	0.0145	−0.0073
3	0.0109	0.0099	0.0010	0.0160	−0.0051
4	0.0412	0.0515	−0.0103	0.0575	−0.0163
5	0.0897	0.0891	0.0006	0.1210	−0.0313
6	0.0896	0.0801	0.0095	0.0880	0.0016
7	0.0692	0.0726	−0.0034	0.0500	0.0192
8	0.1327	0.1516	−0.0189	0.1685	−0.0358
9	0.4031	0.4195	−0.0164	0.5405	−0.1374
10	0.7461	0.7094	0.0367	0.9090	−0.1629
11	0.7800	0.7887	−0.0087	0.8785	−0.0985
12	0.9356	1.0025	−0.0669	0.9905	−0.0549
Mean absolute error			0.0147		0.0475

[1]Equation (9); $k = 4$.
[2]Equation (7); $T = 2$.
[3]Calculated from Table 1 parameters.

Stochastic Comparison

In the deterministic comparison, the catch and fishing effort data were known precisely, the catch per unit effort was always exactly proportional to the average population size, and the population did not fluctuate. However, the stochastic nature of population processes, temporal and spatial changes in the availability and vulnerability of the population to fishing, and the use of sample data to represent an entire fishery all introduce considerable variability in real catch and effort data. Under the assumption that the component sources of variability are independent and random variables with constant expected values and variances, an approximation of the overall variability

TABLE 4.—Estimates of the catchability coefficient, q, by three methods for the weighted and unweighted fishing effort averaging techniques. Actual value of q is 1.0.

Effort averaging method	Integral method[1] Geometric mean	Integral method[1] Arithmetic mean	Difference method[2]
Weighted $\bar{f}^3$	0.8684	1.1949	1.3283
Unweighted $\bar{f}^4$	0.6978	1.3558	2.6606

[1]Equation (22).
[2]Equation (18).
[3]Equation (9); $k = 4$.
[4]Equation (7); $T = 2$.

TABLE 5.—Empirical and estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation approach and two methods of averaging fishing effort.

Method	Replicate	$\hat{m}$	$\hat{Y}_{max}$	$\hat{U}_{max}$	[1]$\hat{q}$	Mean squared error
Empirical	—	[2]0.60	5.60	17.96	1.00	[3]0.0100
Weighted average fishing effort[4]	1	1.03	5.80	17.49	0.53	0.0136
	2	0.00	8.65	18.99	1.56	0.0107
	3	0.60	5.73	17.97	0.87	0.0083
	4	1.04	5.07	18.68	0.95	0.0047
	5	0.24	6.66	18.40	1.13	0.0145
	Mean	0.58	6.39	18.30	1.01	0.0104
	[5]$SE_{\bar{x}}$	0.21	0.62	0.26	0.17	0.0018
Unweighted average fishing effort[6]	1	2.19	6.70	17.10	0.65	0.0110
	2	0.44	6.64	18.62	1.74	0.0130
	3	1.41	6.27	17.54	0.90	0.0100
	4	2.17	6.45	18.06	0.89	0.0095
	5	1.34	6.26	17.79	0.95	0.0117
	Mean	1.51	6.46	17.82	1.03	0.0110
	$SE_{\bar{x}}$	0.32	0.09	0.25	0.19	0.0006

[1]Integral method, geometric mean.
[2]Estimate, Table 1.
[3]Assumed value.
[4]Equation (9); $k = 4$; Program PRODFIT, weighted estimates option.
[5]Standard error of the mean.
[6]Equation (7); $T = 2$; Program PRODFIT, weighted estimates option.

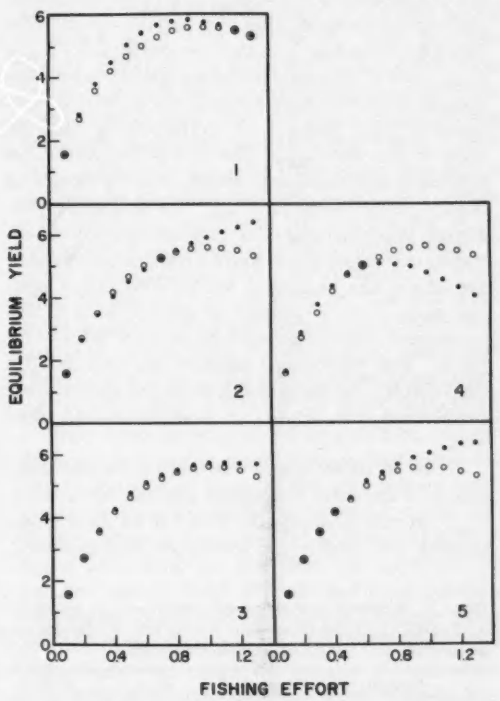

FIGURE 4.—Results (dots) of five stochastic simulated catch trials for the equilibrium approximation approach to fitting the generalized stock production model with the weighted averaging method. Circles are the true values.

structure is the multiplicative error model (Fox 1971)

$$C_i = C_i^* \cdot \epsilon_i \qquad (28)$$

where C_i is the observed catch in year i, C_i^* is the expected catch, and ϵ_i is a random variable with an expected value of 1 and standard deviation σ. In practice, however, the ϵ_i are usually correlated because some (or all) of the component sources of variability do not meet the assumptions.

An ideal (i.e., in the sense that the ϵ_i are independent and random) error structure was chosen to illustrate the estimation ability of the two equilibrium approximation methods, because the "true" error structure of any given population and fishery is unique and largely unknown. Five independent sets of 12 pseudorandom, normally distributed variables, δ, as with an expectation of zero and a standard deviation of 0.1 were produced with the Library Subroutine RAND (University of Washington Computer Center, Seattle). The sets of δ's were used to produce five stochastic catch data sets from the deterministic catch history (Figure 3) and Equation (28), with ϵ_i defined as $1 + \delta_i$.

The results of fitting the five replicate sets of catch and effort data by the weighted (Equation 9) and unweighted (Equation 7) averaging methods are given in Table 5. The effects of even moderate variability on the parameter estimates for both averaging methods are apparent. On the average, two (m and Y_{max}) of the three determining parameters (m, Y_{max}, and U_{max}) are closer to the empirical values for the weighted effort averaging method. The important observation, however, is that all the unweighted estimates of Y_{max} fall above the empirical value and that the average over the five replicates is significantly different from the empirical value with probability greater than 0.999.

Plots of the empirical equilibrium yields and those determined from the generalized stock production model parameters estimated by the weighted average method are compared in Figure 4. Equilibrium yield, for the most part, is estimated reasonably well in each replicate for the range of estimated "equilibrium" fishing effort, 0.0 to 1.0 (Table 3). The exception is replicate 4 where the empirical equilibrium yield is substantially underestimated above $f = 0.8$. Beyond the range of data, $f = 1.0$ to 1.3, the equilibrium yield is estimated reasonably well on the average, but not individually. None of the fitted models, of

course, reveal that there is no equilibrium yield in the range of f = 1.6 to 2.0 for the simulated shrimp population (Figure 2).

Table 6 provides a comparison of the catchability coefficient estimates by three techniques for each fishing effort averaging method. Clearly the best estimates were produced by the geometric mean for the integral method, with the mean estimate by the weighted average fishing effort procedure being slightly better than that of the unweighted average procedure.

TABLE 6.—Estimates of the catchability coefficient, q, from the five replicated stochastic catch histories by three methods for the weighted and unweighted fishing effort averaging procedures. Actual value of q is 1.0.

Effort averaging method	Estimation method	Mean $\hat{q}$	Range of $\hat{q}$
Weighted $\bar{f}$[1]	Integral method[2]		
	Geometric mean	1.008	0.53-1.56
	Arithmetic mean	1.660	1.27-2.41
	Difference method[3]	1.503	1.35-1.77
Unweighted $\bar{f}$[4]	Integral method		
	Geometric mean	1.028	0.65-1.74
	Arithmetic mean	1.546	1.12-2.11
	Difference method	4.459	2.22-10.47

[1]Equation (9); k = 4.
[2]Equation (22).
[3]Equation (18).
[4]Equation (7); T = 2.

COMPARATIVE EXAMPLES OF THE EQUILIBRIUM APPROXIMATION AND TRANSITION PREDICTION APPROACHES

Computer program GENPROD (Pella and Tomlinson 1969) was employed to fit the deterministic and stochastic catch and effort histories of the simulated shrimp to compare the results of the transition prediction and equilibrium approximation approaches. The reader is cautioned, as in the previous section, that these results are largely illustrative and should not be misconstrued as being valid for all cases in which a production model may be employed.

Deterministic Comparison

The comparison of equilibrium parameters in Table 7 reveals that the equilibrium approximation approach provided estimates that were closer to all the empirical values except m, where the two approaches estimated the same value as the empirical equilibrium fit. GENPROD estimated parameters which predicted the simulated catch history (Figure 3) extremely well—the largest error was only 0.05, the sum of squared errors was 0.00659, and the R statistic, a measure of improvement in the fit over simply using the mean catch as a predictor (Pella and Tomlinson 1969), was 0.99994. Utilizing the empirical equilibrium parameters in the generalized production model, however, resulted in a poorer, but still good, prediction of the transition state catches—the maximum error was 0.50, the sum of squared errors was 0.48515, and the R statistic was 0.99544. Apparently due to failure of the assumptions regarding population lag and age structure shifts or problems with precision in the numerical integration, the accuracy of some equilibrium parameter estimates by the transition prediction approach were sacrificed in order to reduce the sum of squared errors by nearly 99%.

Stochastic Comparison

The results of fitting the five replicate stochastic catch histories by the equilibrium approximation and transition prediction approaches are given in Table 8. Of the four common parameters (m, Y_{max}, U_{max}, and q), the equilibrium approximation approach estimates were closer to the empirical values of m, Y_{max}, and q, both on the average and for most of the replicates. The transition prediction approach estimates were closer, on the average, to the empirical value for U_{max}. The transition prediction approach provided one extremely poor estimate of q (replicate 3) and all replicate estimates are above the empirical value—the latter phenomenon could be related to the accuracy of the numerical integration scheme in GENPROD (Fox 1971). The additional parameter required by GENPROD, the ratio of the initial to unexploited population size (P_0/P_{max}), was estimated very well.

There is considerable variability in the estimates of the most frequently desired parameter, Y_{max}, by either approach (Table 8) in spite of assuming an ideal error structure (independent,

TABLE 7.—Empirical and estimated parameters for the simulated pandalid shrimp catch history using the equilibrium approximation and transition prediction approaches.

Approach	$\hat{m}$	$\hat{Y}_{max}$	$\hat{U}_{max}$	$\hat{q}$	$\widehat{P_0/P_{max}}$
Empirical	[1]0.60	5.60	17.96	1.00	1.00
Equilibrium approximation[2]	0.60	5.67	17.97	0.87	—
Transition prediction[3]	0.60	5.92	17.69	1.32	1.16

[1]Estimated, Table 1.
[2]Program PRODFIT, k = 4, unweighted estimates option.
[3]Program GENPROD, KK = 3, DEL = 3, unweighted estimates.

TABLE 8.—Empirical and estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation and transition prediction approaches.

Method	Replicate	$\hat{m}$	$\hat{Y}_{max}$	$\hat{U}_{max}$	$\hat{q}$	$\widehat{P_0/P}_{max}$	Mean squared error
Empirical	—	[1]0.60	5.60	17.96	1.00	1.000	[2]0.0100
Equilibrium approximation approach[3]	1	1.03	5.80	17.49	0.53	—	0.0136
	2	0.00	8.65	16.99	1.56	—	0.0107
	3	0.60	5.73	17.97	0.87	—	0.0083
	4	1.04	5.07	18.68	0.95	—	0.0047
	5	0.24	6.68	18.40	1.13	—	0.0145
	Mean	0.58	6.39	18.30	1.01	—	0.0104
	[4]$SE_{\bar{x}}$	0.21	0.62	0.26	0.17	—	0.0018
Transition prediction approach[5]	1	1.7	5.81	17.72	1.34	0.738	0.0105
	2	0.0	9.09	18.15	1.18	1.095	0.0131
	3	2.1	6.69	17.29	3.97	1.211	0.0086
	4	1.7	5.26	17.83	1.40	1.313	0.0053
	5	0.0	9.34	19.21	1.52	0.797	0.0126
	Mean	1.10	7.24	18.04	1.88	1.031	0.0100
	$SE_{\bar{x}}$	0.45	0.84	0.32	0.52	0.113	0.0014

[1]Estimated, Table 1.
[2]Assumed value.
[3]Program PRODFIT; $k = 4$, weighted estimates option.
[4]Standard error of the mean.
[5]Program GENPROD; KK = 3, DEL = 3, weighted estimates. The program was modified slightly from the version of Pella and Tomlinson (1969) by replacing f_{opt} with Y_{max} as one of the determining parameters to allow fitting the case where $m = 0$ (i.e. $f_{opt} = \infty$ at $m = 0$). Identical solutions were obtained for the remaining three cases with either version.

random and with constant expectation and variance), the observed catch being within 20% of the expected catch with probability 0.95, and the fishing effort being known without error. The maximum error for the equilibrium approximation approach was +54% (replicate 2) and for the transition prediction approach was +67% (replicate 5). The problem with these maximum errors (as well as an additional replicate of the transition prediction approach) was estimating m as 0.0, where Y_{max} occurs at infinite fishing effort. It is not unreasonable, however, to obtain $\hat{m} = 0.0$ since the data series is so short and the best value for m is about 0.60. Considering these results and the true relationship between yield and effort (Figure 2) it would be prudent to adopt an alternative m estimation strategy for short data series.

Alternative strategies which could be adopted for short data series are 1) to consistently assume one of the special cases of the generalized stock production model, either the logistic form ($m = 2$) or the Gompertz form ($m \rightarrow 1$), or 2) fit both special cases and select the one with the least sum of squared errors. Table 9 presents the parameters estimated by the two approaches through fixing the value for m at 1 (actually 1.001) and 2. For comparative purposes, the results of these alternative strategies are summarized in Table 10. Fixing m at 1 or 2 resulted in average estimates of Y_{max} nearer the empirical value with less variability than obtained by allowing m to be freely estimated for both the equilibrium approximation and transition prediction approaches. The empirical value of m is 0.6; hence assuming $m \rightarrow 1$ produced estimates nearer the empirical value of Y_{max} than assuming $m = 2$. For any given data set, however, one could not determine a priori which value of m to assume. The strategy of fitting both $m \rightarrow 1$ and $m = 2$ and then selecting that which provided the least-squares parameter estimates worked very well in comparison with freely estimating m under three criteria: 1) more accurate average estimate, 2) smaller average percentage error, and 3) smaller maximum overestimate. Comparing the equilibrium approximation and transition prediction approaches with the same three criteria reveals that the equilibrium approximation approach was superior [1) 0.5% vs. 5.2%, 2) 3.6% vs. 8.5%, and 3) 3.6% vs. 18.4%)].

DISCUSSION

The simple, illustrative calculations on the simulated pandalid shrimp population, of course, did not determine which of the approaches was better for general use in fitting the generalized stock production model. However, some additional guidance can be gained through examining some of their relative weaknesses with regard to the number of data points and the number of parameters they require.

The moving average of fishing effort in the equilibrium approximation approach results in the exclusion of points at the beginning of the data

TABLE 9.—Estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation and transition prediction approaches for fixed estimates of m.

Method	m	Replicate	$\hat{Y}_{max}$	$\hat{U}_{max}$	$\hat{q}$	$\widehat{P_0/P_{max}}$	Mean squared error
Equilibrium approximation approach[1]	1	1	5.80	17.51	0.54	—	0.0136
		2	5.63	17.99	1.36	—	0.0155
		3	5.56	17.66	0.99	—	0.0087
		4	5.05	18.72	0.92	—	0.0048
		5	5.78	17.73	0.95	—	0.0166
		Mean	5.57	17.92	0.96	—	0.0118
	2	1	6.27	16.73	0.29	—	0.0182
		2	6.27	17.17	1.14	—	0.0267
		3	6.06	16.92	0.88	—	0.0139
		4	5.86	17.65	0.77	—	0.0115
		5	6.35	16.94	1.19	—	0.0260
		Mean	6.16	17.08	0.85	—	0.0193
Transition prediction approach[2]	1	1	5.44	18.18	1.10	0.778	0.0107
		2	6.00	18.16	1.79	1.014	0.0170
		3	6.39	17.81	2.97	1.058	0.0096
		4	4.66	18.08	1.07	1.162	0.0058
		5	6.10	18.40	1.87	0.715	0.0142
		Mean	5.72	18.13	1.76	0.945	0.0115
	2	1	5.95	17.61	1.38	0.720	0.0107
		2	6.47	17.83	2.40	0.962	0.0201
		3	6.63	17.37	3.62	1.210	0.0084
		4	5.30	17.73	1.35	1.361	0.0051
		5	6.51	17.89	2.29	0.604	0.0165
		Mean	6.17	17.69	2.21	0.971	0.0122

[1]Program PRODFIT; $k = 4$, weighted estimates option.
[2]Program GENPROD; KK = 3, DEL = 5, weighted estimates.

TABLE 10.—Summary of Y_{max} estimates by alternative strategies with the equilibrium approximation and transition prediction approaches for five replicated stochastic catch histories. Empirical value of Y_{max} is 5.60.

Method/strategy	$\hat{Y}_{max}$ Mean	Standard error of mean	Average percentage error	Range
Equilibrium approximation approach[1]				
1. Estimate m	6.39	0.62	17.8	5.07-8.65
2. Assume $m \rightarrow 1$	5.57	0.14	3.6	5.05-5.80
3. Assume $m = 2$	6.16	0.09	10.0	5.86-6.35
4. Least-squares, $m = 1$ or 2	5.57	0.14	3.6	5.05-5.80
Transition prediction approach[2]				
1. Estimate m	7.24	0.84	31.7	5.26-9.34
2. Assume $m \rightarrow 1$	5.72	0.31	10.0	4.66-6.39
3. Assume $m = 2$	6.17	0.25	12.4	5.30-6.63
4. Least-squares, $m = 1$ or 2	5.89	0.24	8.5	5.30-6.63

[1]Program PRODFIT.
[2]Program GENPROD.

set unless either there was no fishing prior to the first record of the set or some information is available on the approximate level of catch and effort. One should check carefully to ensure that critical points (those being the only points at high, low, or intermediate levels of fishing) are not excluded or that the fitted model does not deviate greatly from where they might reasonably be expected to lie. If fishing effort was reasonably constant or negligible prior to the first record, dummy data of length $k - 1$ can be employed to allow use of the first few data points. Also, since the average fishable duration, T, is less than the number of significant fishable year classes, k, the unweighted averaging method will result in fewer data being excluded In any case, the sensitivity of the parameter estimates to alternative averaging times should be explored.

No data points are excluded with the transition prediction approach, a positive factor which should be considered even if one is satisfied with the parameter estimates obtained with the equilibrium approximation approach. On the other hand, the transition prediction approach utilizes five parameters while the equilibrium approximation approach utilizes only three, so that with few significant year classes in the fishable population there is little difference between the required number of data points. For example, the transition prediction approach statistically

requires six points, while the equilibrium approximation approach with four significant year classes will require, in general, seven points. With a large number of significant year classes in the fishable population or a relatively high age at first capture, however, the major concern for either approach is the likelihood of failure of the transition state population assumptions.

The results summarized in Table 7 illustrate a general shortcoming in simultaneously estimating a large number of parameters, i.e. large deviations from model can be statistically reduced in a least-squares estimation procedure at the expense of the accuracy of certain "desired" parameters. The transition prediction approac , fitting a "free-form" type of curve with five parameters, is relatively more susceptible than the equilibrium approximation approach which fits a monotonically decreasing curve with only three parameters. On the other hand, estimates from the equilibrium approximation approach can be very sensitive to the placement of one data point in certain cases (e.g., a data point at an intermediate level of fishing with clusters of points at both low and high levels of fishing).

Utilizing the production model approach for assessing the effects of exploitation presents significant problems in addition to choice of the parameter estimation procedure or the length of the data series. These additional problems are 1) maintaining a constant catchability coefficient throughout the data series, 2) assessing the effects of changes in the constitution of the fishery, and 3) assessing the effects of time lags in population production processes.

The basic components of the overall effective catchability coefficient are 1) the relative efficiency of various types and classes of fishing gear and 2) the manner in which the gear is employed relative to the availability and vulnerability of the population, and its subunits, to capture. Heterogeneity in the efficiency of various gear classes, or vessels, within a fishing season can be alleviated by adjusting for their estimated relative fishing powers—currently the best method for estimating fishing power is by analysis of variance with the computer program FPOW (Berude and Abramson 1972). The major problem remaining, however, is adjusting for among-year changes in efficiency of the standard gear. Rothschild (1970) discussed and provided examples of problems associated with changes in the catchability coefficient related to areal deployment of the fishing gear. The expansion of fishing across a gradient of population density will increase or decrease the effective catchability coefficient depending on the direction of the density gradient and fishing expansion. Year-to-year shifts in the population location and density relative to the fishing effort deployment also could likewise create trends in the catchability coefficient. Age-specific differences in the catchability would cause shifting of the overall effective catchability coefficient with changes in fishing effort. For example, if the catchability of fish declined with age, then the overall effective catchability of the fishable population would increase with increasing fishing effort since the relative proportion of younger age groups would most likely increase.

Alterations in the constitution of the fishery probably are the most difficult problems to overcome satisfactorily. Expansion of the fishery across several stocks, either independent or with some mixing, can result in rather large shifts in the productivity estimates (Joseph 1970; Inter-American Tropical Tuna Commission 1972). Changes in the relative levels of fishing effort exerted by different gear types which exploit different age groups of the population, either voluntarily or through a change in minimum size limit regulations, can similarly have significant impact on the shape of the production model curve (Lenarz et al. 1974). The latter problem identifies a major shortcoming of the production model approach; i.e., the impact on total yield by altering the selectivity of fishing gear can not be assessed a priori without considerable additional information.

The effects of time lags in population production processes (e.g., reproduction, growth, and mortality, both density-independent and density-dependent) can result in either overestimation or underestimation of the population productivity, or in population cycling which may never result in reaching an equilibrium state (Wangersky and Cunningham 1957; Walter 1973).

In summary, both the equilibrium approximation and the transition prediction fitting methods are useful, one or the other more so under conditions outlined above. Application of the production model to catch and fishing effort data is relatively simple, the primary virtue of the approach. The interpretation of the results and the formulation of advice for managing the resource, however, can be extraordinarily complicated by a variety of

factors. Therefore, the proper perspective of production model analysis is that it is little more than a regression model, yet very useful for making "first estimate" projections of the relationship between the level of exploitation and expected equilibrium yield.

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APPENDIX

Miscellaneous Equations for PRODFIT

Elements of the X-matrix

Let $\hat{U}_i = (\alpha + \beta \bar{f}_i)^{1/(m-1)}$

Then

$$\frac{\partial \hat{U}_i}{\partial \alpha} = 1/(m-1)\,(\alpha + \beta \bar{f}_i)^{(2-m)/(m-1)}$$

$$\frac{\partial \hat{U}_i}{\partial \beta} = \bar{f}_i \times \frac{\partial \hat{U}_i}{\partial \hat{\alpha}}$$

$$\frac{\partial \hat{U}_i}{\partial m} = -(\alpha + \beta \bar{f}_i)^{1/(m-1)} \times \ln(\alpha + \beta \bar{f}_i)[1/(m-1)]^2$$

Derivatives for the Delta Method Variance Estimates

Y_{max}

$$\frac{\partial Y_{max}}{\partial \alpha} = Y_{max}[m/(m-1)]/\alpha$$

$$\frac{\partial Y_{max}}{\partial \beta} = -Y_{max}/\beta$$

$$\frac{\partial Y_{max}}{\partial m} = Y_{max} \times \ln(m/\alpha)/(m-1)^2$$

f_{opt}

$$\frac{\partial f_{opt}}{\partial \alpha} = (1/m - 1)/\beta$$

$$\frac{\partial f_{opt}}{\partial \beta} = -\alpha/\beta^2\,(1/m - 1)$$

$$\frac{\partial f_{opt}}{\partial m} = -\alpha/(\beta m^2)$$

U_{opt}

$$\frac{\partial U_{opt}}{\partial \alpha} = U_{opt}/[\alpha(m-1)]$$

$$\frac{\partial U_{opt}}{\partial m} = -U_{opt}\,[m \ln(\alpha/m) + m - 1]/[m(m-1)^2]$$

NET PHYTOPLANKTON AND THE GREATER THAN 20-MICRON PHYTOPLANKTON SIZE FRACTION IN UPWELLING WATERS OFF BAJA CALIFORNIA

THEODORE J. SMAYDA[1]

ABSTRACT

Between 26 March and 6 April 1973 various phytoplankton studies were carried out during the MESCAL II survey in an area measuring circa 105 km × 30 km, and centered approximately at Punta San Hipolito, Baja California. Upwelling was then in its early stages. The composition of 22 collections of net phytoplankton (No. 20 net), and the composition and abundance of the non-setose (i.e., excluding *Chaetoceros*, *Bacteriastrum*) size fraction >20 μm collected at various depths at 13 stations are reported here. The mean carbon content in the upper 50 m contained in the >20 μm non-setose size fraction was 533.5 mg C/m³ for all stations, and ranged from 306 to 1,022 mg C/m³ at individual stations. Based on a C/Chl *a* ratio of 40:1, the mean concentration in the euphotic zone represents circa 12% of the total phytoplankton carbon present. *Lauderia annulata* (28%) and several *Coscinodiscus* species (33%) accounted for most of the carbon found in the >20-μm size fraction, even though the latter comprised only about 10% of the mean population expressed as cell number. The mass occurrence of *Coscinodiscus* reported previously for Magdalena Bay during summer upwelling was not observed. The *Coscinodiscus* population and the non-setose component of the >20- μm size fraction contributed only 1.2% and 4%, respectively, of the daily caloric ingestion estimated for the crab, *Pleuroncodes planipes*, previously reported to graze heavily on *Coscinodiscus*. Sinking rates (61 to 144 m/h) of *Pleuroncodes* fecal material exceeded by onefold to fourfold those rates estimated for the various sizes of *Coscinodiscus* and zooplankton fecal pellets sampled during the survey. The abundant crab population is, thus, important in causing an exceptionally rapid deposition of unassimilated phytoplankton frustules and organic material onto the sea floor. Floristic changes accompanying upwelling were detectable. The occurrence of the unique diatoms *Coscinodiscus* (*Brenneckella*) *eccentricus* and *Planktoniella muriformis* in these waters is apparently reported for the first time. The present data together with earlier observations suggest that the net diatom community is similar in the coastal waters extending from San Diego, Calif., to the Gulf of Panama. The data do not support the idea that the abundance of *Pleuroncodes* in this upwelling system is causally linked to that of *Coscinodiscus*.

There is little information on the composition and abundance of the phytoplankton community in the upwelling waters off Baja California. The available data are mostly qualitative (Allen 1924, 1934, 1938; Balech 1960; Cupp 1930, 1934), aside from recent, cursory observations on phytoplankton cells >25 μm which are grazed by the red crab, *Pleuroncodes planipes* (Longhurst et al. 1967).

Unique mass blooms of *Coscinodiscus* have been observed by Longhurst et al. in the upwelled waters of Magdalena Bay. This phenomenon and the great abundance of *Pleuroncodes*, which grazes on *Coscinodiscus* cells, may be distinctive characteristics of this upwelling system. Smith et al.[2] have concluded that this crab is an important herbivore in the California Current upwelling system, where its role is comparable to that of the anchovy, *Engraulis ringens*, in the Peru Current. Longhurst (1968) has evaluated the potential fishery for this galatheid crab, which occurs in both the benthic and pelagic zones; some crabs exhibit diurnal migrations (Longhurst et al. 1967).

Pleuroncodes is generally distributed throughout this region (Blackburn 1969), while information on the regional distribution and abundance of *Coscinodiscus* is lacking. It is therefore unknown whether *Coscinodiscus* indeed generally characterizes the phytoplankton community in these upwelled waters. Clarification of this is relevant

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[2]Smith, K. L., Jr., G. R. Harbison, G. T. Rowe, and C. H. Clifford. Respiration and chemical composition of *Pleuroncodes planipes* (Decapoda: Galatheidae): Energetic significance in an upwelling system. Manuscr., 22 p. Woods Hole Oceanogr. Inst., Woods Hole, Mass.

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to the question of whether *Pleuroncodes*' occurrence is causally linked to that of *Coscinodiscus*.

Coscinodiscus and other heavily silicified diatoms sink to the sea floor, as documented for the Gulf of California (Round 1967, 1968). This deposition contributes skeletal remains (i.e., to the thanatocoenosis) and organic matter to the sediments. The abundance and sinking characteristics of this diatom population are also of interest, since *Pleuroncodes* also occurs in the benthos. During this benthic residence, when population densities up to 250 individuals/m² have been found (Smith et al. footnote 2), it may feed on detrital material (Longhurst et al. 1967).

Various studies on phytoplankton were carried out during the MESCAL II expedition of the RV *Thomas G. Thompson* in 1973 to study upwelling off Baja California, as a continuation of 1972 activities in this area (Walsh et al 1974). These included the routine, shipboard examination of both net phytoplankton and the >20-μm size fraction filtered from quantitative samples. The discovery that natural populations of a *Ditylum brightwelli* and, possibly, *Biddulphia mobiliensis* exhibited diel cell division has been reported (Smayda in press a).

Examination of the >20-μm size fraction was partly motivated by the need to know its composition and abundance, particularly that for *Coscinodiscus*. This was to evaluate the aforementioned relationship possibly occurring between *Pleuroncodes* and *Coscinodiscus*, and to establish the latter's importance during the initial stages of upwelling. This latter objective was prompted by the remarkable bloom found in Magdalena Bay during a later stage of the upwelling cycle. Finally, such data are needed to evaluate the sinking and turnover rates of the more heavily silicified and dissolution-resistant components of this size fraction which sink faster and represent an energy source for benthic secondary production.

METHODS

Between 26 March and 6 April 1973, 22 collections of net phytoplankton were made at 15 stations (multiple sampling on different days at some). A No. 20 (mesh opening of 69 μm) net 30 cm in diameter sampled the upper 50 to 100 m (depending on depth) for 30 min by repeated vertical oscillations, during which the net was lowered at a rate of ca. 30 m/min and retrieved at a rate of 10 m/min. The samples were examined microscopically soon after collection, after placing onto a slide an aliquot of the unpreserved, sedimented material from an unagitated sample.

Of the 15 stations sampled, 13 were located in a sampling block measuring about 105 km long and 30 km wide centered approximately at Punta San Hipolito off the coast of Baja California (Figure 1). The coordinates of the northern- and southernmost stations are lat. 27°6.7′N, long. 114°21.2′W and lat. 26°28.5′N, long. 113°45.5′W, respectively. The stations extended offshore from within sight of land to within, or near, the California Current; the inner- and outermost stations were at lat. 26°55.2′N, long. 114°02.2′W and lat. 26°51.2′N, long. 114°10.7′W, respectively. Stations 1 and 2 (not shown in Figure 1) were located about 460 km north of this main sampling area at lat. 30°57.8′N, long. 116°32′W and lat. 28°8.2′N, long. 115°39.2′W, respectively.

Quantitative samples were also collected at 13 stations from the surface to 50 m at 10-m intervals, and at 75 m with 5-liter Niskin Bottles. Seven stations (18 to 24) were sampled at 6-h intervals while following a drogue. From samples collected in the upper 30 m, 2 liters were usually filtered through a 20-μm mesh net, and 3 liters from greater depths. The apparatus used is illustrated in Durbin et al. (in press). The material

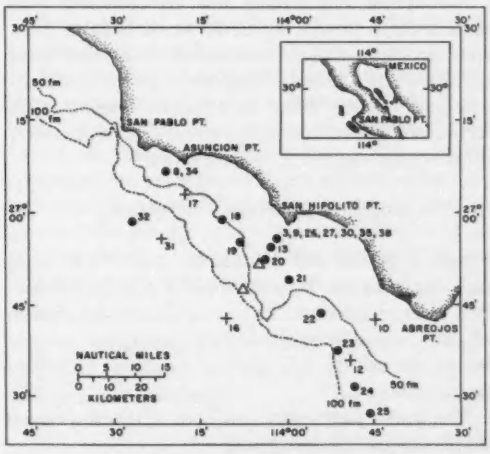

FIGURE 1.—Location of stations where collections of net phytoplankton (+) and net and water bottle samples (•) were made from 26 March to 6 April 1973 (except that net and water bottle collections were made only at Stations 26 and 38 at the frequently sampled station located off Punta San Hipolito). △ represents stations, along with Station 27, used to illustrate the occurrence of upwelling in Table 1; the outermost station is Station 29.

retained by the net was concentrated to 30 ml, preserved with hexamine + Formalin[3] and 1 ml of the concentrate then enumerated on board ship using a Sedgwick Rafter Counting Chamber. The concentrate was obtained by stopping filtration to leave about 1 cm of water above the filter.

As stated in the Introduction, cells in the size class >20 μm are frequently heavily silicified and sink to the sea bed. *Chaetoceros* and *Bacteriastrum* are usually not represented in the latter (Round 1968), presumably because of rapid dissolution of their silicon frustules. The various objectives of the present and other, ongoing studies during MESCAL II emphasized the *Coscinodiscus* and other non-setose genera, and also required real-time data for proper execution of the program. Shipboard enumeration of phytoplankton was therefore necessary. Quantitative shipboard enumeration of specimens belonging to genera characterized by setae is difficult; their setose nature makes them prone to movement within the counting chamber in response to the ship's vibrations and movement. For these various reasons, during the numerical census representatives of the genera *Chaetoceros* and *Bacteriastrum* and a species similar in general appearance to (but probably not) *Nitzschia frigida* were not enumerated.

Numerical abundance was transformed into carbon equivalents. From 10 to 40 cells of each species (depending on abundance) were measured to obtain the mean dimensions required to calculate cell volume using appropriate mensuration formulae. The carbon content was then calculated from Strathmann's (1967) equation

$$\log C = 0.758 (\log V) - 0.352$$

where V is the cell volume in μm^3. From this cellular estimate (pg per cell), the population carbon was computed. The constant 0.352 differs slightly from Strathmann's given value, and is based on additional diatom analyses (Eppley, pers. commun.).

The mean population per liter ($\bar{C}$) in the upper 50 m was calculated from:

$$\bar{C} = \frac{1}{2Z_5} [(C_0 + C_1)(Z_1 - Z_0) + (C_1 + C_2)(Z_3 - Z_2) + \ldots + (C_4 + C_5)(Z_5 + Z_4)]$$

where C_0, C_1, etc. are the observed cell (carbon) concentrations per liter at the surface (Z_0) and 10 m (Z_1), etc., down to 50 m (Z_5). Concentrations per square meter of sea surface down to 50 m were obtained from ($\bar{C}$) (5×10^4). Samples were collected at 75 m at only 9 of the 13 quantitative stations because of depth. This, together with the sparse populations usually found there, accounts for the emphasis on the upper 50 m.

RESULTS

Upwelling occurred during the field program. Table 1 presents some representative physical and chemical parameters along a transect of three stations sampled on 3 and 4 April near Punta San Hipolito (Figure 1). The inflow and upwelling of cold, nutrient-rich water at the nearshore station (27) is evident. Upwelling was usually more pronounced near and shorewards of the 50-fathom isobath. Details of this upwelling, which was in its early stages, and associated biotic responses will be presented elsewhere (Walsh, Kelley, Whitledge, Huntsman, and Pillsbury in prep.).

Net Phytoplankton

The species identified in the net material are listed in Appendix Table 1. Throughout the ship's track of ca. 700 km the No. 20 net phytoplankton was characterized by the genus *Chaetoceros*

TABLE 1.—Hydrographic conditions along a transect off Punta San Hipolito showing the occurrence of upwelling during 3 and 4 April 1973 (Stations shown in Figure 1).

Depth (m)	°C	‰	σ_t	μg at/liter PO_4	NO_3	SiO_2
Station 29 (lat. 26°48'N, long. 114°07.5'W) 0220						
0	16.04	34.122	25.08	0.47	0.98	1.23
10	16.04	34.119	25.08	0.54	0.98	1.10
20	15.67	34.127	25.17	0.55	0.98	0.98
30	15.65	34.112	25.16	0.63	1.31	1.53
40	13.68	33.957	25.47	1.05	3.94	7.52
50	11.87	33.736	25.65	1.40	9.18	13.34
75	11.51	33.821	25.79	1.65	14.43	18.83
Station 28 (lat. 26°51.5'N, long. 114°04.8'W) 0100						
0	15.69	34.044	25.10	0.51	0.66	1.75
10	15.25	34.002	25.17	0.63	0.66	2.48
20	14.35	33.912	25.29	0.82	1.31	4.91
30	13.64	33.930	25.45	1.06	3.94	8.52
40	11.94	33.690	25.60	1.22	8.20	11.29
50	11.84	33.922	25.80	1.67	14.43	16.95
Station 27 (lat. 26°55.2'N, long. 114°02.2'W) 1720						
0	13.53	34.080	25.59	1.15	7.03	11.87
10	13.26	34.086	25.65	1.32	7.91	12.39
20	13.04	34.092	25.70	1.57	10.94	15.36
30	12.26	34.063	25.83	1.83	14.28	18.85
40	11.81	34.141	25.98	2.12	20.06	22.68
50	11.36	34.243	26.14	2.34	23.72	27.05

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(*affinis, curvisetus, debilis, didymus, socialis*) in species and abundance. The genus *Coscinodiscus* was a conspicuous co-dominant, but varied in relative abundance from station to station. The remarkable colonial diatom *Planktoniella muriformis* (Loeblich et al. 1968; Round 1972) was also prominent throughout this region. Nonetheless, some apparent regional differences are noteworthy.

At Station 1 located near Punta Kolnett a very rich, diverse net plankton community occurred on 26 March dominated by *Chaetoceros* and *Nitzschia* spp. and *Thalassiothrix frauenfeldii*. *Asterionella japonica*, *Eucampia cornuta*, and *Lithodesmium undulatum* were other abundant diatoms. This community stands out from others in the importance of *Asterionella* (many small pennate diatoms were attached to the colonies), which was not found in subsequent net tows. Also unlike subsequent stations, *Phaeocystis* cf. *pouchetii* was common while *Coscinodiscus* spp. were not. Allen (1945) has reported extensive blooms of *Phaeocystis* off southern California. This colonial haptophycean is well known for its apparent adverse effects on certain fisheries in the North Sea during mass blooms.

The lack of nutrient data at Stations 1 and 2 prevents assessment of possible upwelling. However, when sampled on 27 March the upper 50 m of the latter station was considerably warmer (15.29°C at 0 m, 14.94°C at 50 m) than at Station 1 (14.53°C at 0 m, 11.42°C at 40 m). The net phytoplankton community was considerably poorer and dominated by *Ceratium* spp.; peridinians were frequent, and the diatoms *Biddulphia mobiliensis*, *Coscinodiscus* spp., and *Planktoniella sol* were common. This community suggests that upwelling was weak, if occurring.

The principal features of the net collections (n = 20) made in the intensive survey area (Figure 1) are: 1) the community at the deepwater stations (16, 31, 32) located seaward of the 50-fathom isobath was less abundant and differed somewhat relative to the shallower stations; 2) the composition at the latter stations was generally similar; and 3) a slight change in apparent species dominance occurred by the end of the 12-day sampling period.

At the outer, deepwater Station 16 (30 March) *Chaetoceros affinis* and *curvisetus* dominated; *Ceratium* and *Peridinium* spp. were also common. At Stations 31 and 32 (4 April), *Bacteriastrum* dominated together with the above *Chaetoceros* species and *decipiens* and *socialis*. *Coscinodiscus* spp. were subordinate; *Asterolampra marylandica* and cf. *Pyrocystis lunula* were frequent. The lower relative abundance and the difference in dominant species at these outer stations are also reflected in the quantitative samples (Table 2). The lowest mean concentration occurred at Station 32 (quantitative samples were not collected at Stations 16 and 31). The physical-chemical data indicate that upwelling was not occurring at Station 16 and was insignificant, if taking place, at Stations 31 and 32.

At the nearshore Station 34 (4 April), where the hydrographic conditions were similar to Station 27 (Table 1), the *Bacteriastrum* component important at Stations 31 and 32 was absent and *Thalassiosira rotula* dominated along with the *Chaetoceros* spp. This increased importance of *Thalassiosira rotula* relative to samples collected a week earlier is also noted in the series collected near Punta San Hipolito (Stations 3 to 38) (Figure 1). The nearshore communities were otherwise dominated by different proportions of *Chaetoceros* and *Coscinodiscus* spp. The *Coscinodiscus* component was especially prominent at Stations 10, 17, and 19, for example. (The net tows frequently contained pennate diatoms which might have been scoured from bottom sediments during upwelling.)

The apparent differences in net community composition, abundance, and species succession during the 10-day sampling period in the intensive survey area probably reflect variations in intensity of upwelling, which was just beginning based on aerial reconnaissance of sea-surface temperatures prior to the ship's arrival in the survey area. Between 28 March (Station 3) and 30 March (Station 13) cold water ascended 10 m at the fixed station near Punta San Hipolito (Figure 1; Pillsbury, pers. commun.).

Quantitative Samples

Numerical Abundance

The results of the quantitative census of the non-setose species in the >20-μm size fraction are presented in Table 2. The mean population level in the upper 50 m ranged from about 2,110 to 9,800 cells/liter. *Lauderia annulata* dominated numerically (from 35 to 60% of total abundance) throughout the area, except at the last station (38) sampled (3%) where *Thalassiosira rotula* dominated

TABLE 2.—The mean, non-setose population (cells/liter and μg C/liter) in the >20-μm size class in the upper 50 m. Lower value in cell abundance (i.e. *n/n*) represents number of dead cells.

Station	Time	Σ cells/carbon	*Actinoptychus undulatus*	*Bidulphia mobiliensis*	*Ceratium* spp.	*Coscinodiscus (Brenneckella) eccentricus*	Σ *Coscinodiscus* spp.	*Ditylum brightwelli*	*Eucampia cornuta*	*Guinardia flaccida*	*Lauderia annulata*	*Lithodesmium undulatum*	*Planktoniella muriformis*	*Planktoniella sol*	*Rhizosolenia* spp.	*Schroederella delicatula*	*Thalassiosira rotula*	OTHERS	% dead cells of *Coscinodiscus* spp.
13	1145	4,067	29/5	115/1	119	33	630/54	198/7	24	3	2,015/2	330	32	308/25	5/1	173	48	5	8.5
		11.05	0.07	0.72	0.25	0.08	4.83	1.49	0.01	0.01	2.68	0.48		0.20		0.17	0.06		
18	1800	3,995	47/6	254/15	29	35	631/49	284/5	57	16	1,396	589	87	335	3	177	48	7	7.8
		13.85	0.11	1.58	0.06	0.09	6.61	2.14	0.02	0.07	1.86	0.85		0.22		0.18	0.06		
19	0000	4,576	94	171	12	30	520/63	267	14	43	2,942	508	31	220	6	448/17	24	5	11.5
		16.13	0.23	1.06	0.02	0.08	7.26	2.01	0.004	0.18	3.92	0.74		0.15		0.45	0.03		
20	0600	3,321	22/3	59/2	12	7/1	309/27	125	2	22	2,008	306	20	197/3	5	116/34	114	3	8.7
		7.38	0.05	0.37	0.02	0.02	2.38	0.94	0	0.09	2.67	0.44		0.13		0.12	0.15		
21	1200	2,456	29/2	66/2	5	29	332/35	137	—	37	1,171/2	181/18	28	194/5	36/2	168	37	4	10.5
		8.31	0.09	0.42	0.01	0.07	4.37	1.03	—	0.15	1.56	0.26		0.13		0.17	0.05		
22	1800	9,806	45	232	10	55	479/29	552/15	123	91	5,665	719	37	746	11	841/19	190	10	6.1
		20.44	0.11	1.44	0.02	0.14	3.96	4.16	0.04	0.38	7.55	1.04		0.50		0.85	0.25		
23	0000	4,476	26/1	76/2	10	40	318/50	148/2	77	94	2,512	425	36	288/12	130/2	236/50	56	4	15.7
		8.96	0.06	0.47	0.02	0.10	2.27	1.16	0.02	0.39	3.35	0.62		0.19		0.24	0.07		
24	0600	3,595	21/1	80/2	17	97	191/17	64	—	101	1,957/10	314	7	538/13	52	113	38/5	5	8.9
		7.11	0.05	0.50	0.04	0.24	1.79	0.48	—	0.42	2.61	0.46		0.36		0.11	0.05		
25	1200	4,915	48	76	36	44	257/42	179	190	42	2,616	461	30	569	28	276	46	17	16.3
		9.13	0.12	0.47	0.07	0.11	1.90	1.35	0.06	0.18	3.48	0.67		0.38		0.28	0.06		
26	1800	3,248	26/2	88	1	12	508/50	78/2	10	8	1,526	148	6	46	—	170	618	3	9.8
		7.75	0.06	0.55	0	0.03	3.23	0.59	0.003	0.03	2.03	0.21		0.03		0.17	0.82		
32	1800	2,110	8	59	43	101/1	230/43	53/1	—	109	819	120	6	552	29	7	10	7	18.7
		6.12	0.02	0.37	0.09	0.25	2.88	0.40	—	0.46	1.09	0.17		0.37		0.01	0.01		
34	2140	8,653	10/2	54/1	12	11	406/16	272	46	43	3,835	486	12	151/2	7	1,318	1,990	—	3.9
		15.00	0.02	0.34	0.02	0.03	2.47	2.05	0.01	0.18	5.11	0.70		0.10		1.33	2.64		
38	0720	4,926	53/2	6	49	4	623/65	40	18/60	26	136/7	602/19	8	82	5	618	2,639/2	17	10.4
		9.03	0.13	0.04	0.10	0.01	3.10	0.30	0.005	0.11	0.18	0.87		0.05		0.62	3.51		
																			$\bar{x}$ = 10.5

(54%). The latter was also important at Station 34 (28%); the maximum, mean abundance of *Schroederella delicatula* (1,318 cells/liter) was also found here. *Coscinodiscus* spp. were usually next to *Lauderia* in numerical importance, and composed a maximum of 10 to 15% of the mean population. Table 3 lists the species of *Coscinodiscus* found. (*Coscinodiscus* "large species" may represent several species difficult to identify properly in the counting chamber.) *Planktoniella sol* contributed from about 2 to 25% of the mean population, and *Lithodesmium undulatum* usually around 7 to 12%.

The absolute abundance of the unique colonial aggregate, *Planktoniella muriformis*, which can have up to at least 530 cells/colony (Loeblich et al. 1968), is unknown; individual cells in the colonies were not counted. The mean number of colonies per liter in the upper 50 m ranged from 6 to 92, with the low levels (6 to 10) persistent at stations made after Station 25 (Table 2). The mean vertical distribution of this species shows a similar abundance (22 to 30 colonies/liter) in the upper 40 m (Table 4; Figure 2), contrary to expectations, and will be reconsidered later.

Species of *Rhizosolenia* >20 μm were not abundant, and included: *bergoni*, *calcar avis*, *imbricata* var. *shrubsolei*, *stolterfothii*. Diatoms which are included in OTHERS in Table 2, and their maximum abundance (cells per liter) are:

Asteromphalus heptactis (12)
Corethron pelagicum (19)
Dactyliosolen sp. (72)
Hemidiscus cuneiformis (84)
Leptocylindrus danicus (228)
Paralia sulcata (79)
Skeletonema costatum (152)
Stephanopyxis cf. *turris* (192)
Thalassionema nitzschioides (126)
Thalassiothrix cf. *mediterranea* var. *pacifica* (16)

TABLE 3.—The mean population as cells/liter (a) and μg C/liter (b) of the different *Coscinodiscus* species >20 μm in the upper 50 m.

Station		*(Brenneckella) eccentricus*	cf. *asteromphalus*	? *concinnus*	*eccentricus*	cf. *granii*	"large species"	Σ
13	a	33	118	3	465	3	41	663
	b	0.082	0.568	0.015	1.361	0.061	2.822	4.91
18	a	35	209	95	262	2	63	666
	b	.087	1.005	.467	.767	.041	4.337	6.70
19	a	30	202	103	135	4	77	551
	b	.075	.972	.506	.395	.062	5.300	7.33
20	a	7	152	36	104	0	17	316
	b	.017	.731	.177	.304	0	1.170	2.40
21	a	29	182	18	94	5	44	372
	b	.072	.876	.088	.275	.102	3.029	4.44
22	a	55	204	57	184	5	30	535
	b	.137	.981	.280	.539	.102	2.065	4.10
23	a	40	144	28	116	10	13	351
	b	.100	.692	.138	.340	.205	.895	2.37
24	a	97	64	51	64	4	14	294
	b	.241	.308	.251	.187	.082	.964	2.03
25	a	44	167	13	64	1	12	301
	b	.109	.803	.064	.187	.020	.826	2.01
26	a	12	176	18	283	11	18	518
	b	.030	.847	.088	.828	.225	1.239	3.26
32	a	101	125	17	42	34	20	339
	b	.251	.601	.084	.123	.696	1.377	3.13
34	a	11	95	24	271	0	16	417
	b	.027	.457	.118	.793	0	1.101	2.50
38	a	4	60	19	528	0	17	628
	b	.009	.289	.093	1.545	0	1.170	3.11

These species are listed only to indicate their presence; their actual abundance is probably greater, since most of these would routinely pass through a 20-μm mesh net depending on orientation of the cells during filtration.

Ceratium furca usually dominated the dinoflagellates >20-μm; populations of *Ceratium fusus* were persistent. Reproductive stages similar to those depicted by von Stosch (1964) for some ceratians were frequent. *Pyrocystis* was present, including an organism quite reminiscent of *Pyrocystis lunula* (vide Figure 559 in Schiller 1937) in shape and stages found. Maximum abundance was 60 cells/liter in the upper 10 m at Station 38 (13.96° to 14.31°C, otherwise similar to Station 27 (Table 1)). Various stages of the cf. *Pyrocystis lunula* cycle were also found during growth experiments carried out with mixed, natural populations. The dinoflagellate population was usually sparse, however, with no indication of red tide in the >20-μm size fraction either visually or microscopically. However, several weeks later, following temporary subsidence of upwelling, a red-tide outbreak occurred in these waters (Walsh, pers. commun.) similar to pre-upwelling blooms encountered during MESCAL I in March 1972 (Walsh et al. 1974).

A coccolithophorid similar to *Syracosphaera apsteini* (15 cells/liter) was found occasionally.

Noctiluca scintillans was frequently encountered in the samples, especially at Station 38, with evidence of active predation of the phytoplankton by *Noctiluca*.

Carbon Abundance

The mean carbon content in the upper 50 m for the dominant non-setose diatom component >20 μm, exclusive of *Planktoniella muriformis, Rhizosolenia* spp., and OTHERS is given in Table 2. The reason for excluding *Planktoniella muriformis* is because of the great difficulty to enumerate the cells within the colonies, whose size varied considerably. Insufficient specimens of the rarer *Rhizosolenia* and "other" species prevented reliable cell sizing to calculate cell volume.

The mean carbon content in the upper 50 m ranged from 6.12 to 20.44 μg C/liter at the various stations; the overall mean was 10.67 μg C/liter (Tables 2 to 4). Comparison of the percent of the total population represented by a species on a numerical and carbon basis shows an inherent inadequacy of the numerical census as a population monitor. For example, the *Coscinodiscus* spp. as carbon contributed from 16.7 to 53.4% of that in the >20-μm size fraction (exclusive of the non-setose species which were not monitored), while numerically they composed only from 4.8 to 16.7%. The corresponding means for all stations were about 36% and 11%, respectively. The six most abundant species as carbon ($\bar{x}$ = 10.67 μg C/liter) compared to their numerical ($\bar{x}$ = 4,732 cells/liter) importance in the upper 50 m are:

	μg C/liter	%	cells/liter	%
Lauderia annulata	2.97	27.8	2,227	47
Coscinodiscus "large species"	1.84	17.2	27	0.6
Ditylum brightwelli	1.38	12.9	184	3.9
Coscinodiscus cf. *asteromphalus*	0.71	6.7	148	3.1
Biddulphia mobiliensis	0.64	6.0	103	2.2
Thalassiosira rotula	0.61	5.7	454	9.6

For *Coscinodiscus* (*Brenneckella*) spp., the means are 3.53 μg C/liter (33.1%) and 458 cells/liter (9.7%). The *Coscinodiscus* (*Brenneckella*) spp. and the four other species given above compose 9.13

TABLE 4.—Mean vertical distribution as cells/liter and as equivalent carbon (μg C/liter) of the >20- μm non-setose size fraction at all stations between 30 March and 6 April 1973 in MESCAL II survey area (n = 12 (0 m), n = 13 (10-50 m), n = 9 (75 m))

Species	Depth (m)							$\bar{x}$ upper 50 m
	0	10	20	30	40	50	75	
Actinoptychus undulatus	36	41	48	36	18	13	8	34
	0.08	0.10	0.12	0.09	0.04	0.03	0.02	0.081
Biddulphia mobiliensis	177	185	121	66	47	19	5	103
	1.10	1.15	0.75	0.41	0.29	0.12	0.03	0.64
Ceratium spp.	66	68	28	5	0	2	0	27
	0.14	0.14	0.06	0.01	0	0.005	0	0.057
Coscinodiscus (Brenneckella) eccentricus	73	67	43	22	17	9	2	38
	0.16	0.17	0.11	0.05	0.04	0.02	0.005	0.092
Coscinodiscus cf. *asteromphalus*	286	228	150	96	112	18	33	148
	1.38	1.10	0.72	0.46	0.54	0.09	0.16	0.709
Coscinodiscus ? concinnus	49	64	46	13	30	17	16	37
	0.24	0.31	0.23	0.06	0.15	0.08	0.08	0.182
Coscinodiscus eccentricus	296	346	254	151	85	62	15	203
	0.87	1.01	0.74	0.44	0.25	0.18	0.04	0.593
Coscinodiscus cf. *granii*	11	8	3	10	2	2	0	6
	0.23	0.16	0.06	0.20	0.04	0.04	0	0.119
Coscinodiscus ("large species")	26	28	60	16	15	3	5	27
	1.79	1.93	4.13	1.10	1.03	0.21	0.34	1.838
Σ *Coscinodiscus (Brenneckella)*	741	741	556	308	261	111	71	458
	4.67	4.68	5.99	2.31	2.05	0.62	0.63	3.53
Ditylum brightwelli	304	346	247	98	73	3	4	184
	2.29	2.61	1.86	0.74	0.55	0.02	0.03	1.38
Eucampia cornuta	85	24	28	85	33	6	0	43
	0.03	0.01	0.01	0.03	0.01	0	0	0.015
Guinardia flaccida	69	109	66	24	17	2	0	50
	0.29	0.46	0.28	0.10	0.07	0.008	0	0.211
Lauderia annulata	3,393	3,761	3,597	1,479	580	46	30	2,227
	4.52	5.01	4.79	1.97	0.77	0.06	0.04	2.97
Lithodesmium undulatum	584	667	589	259	211	42	8	408
	0.85	0.97	0.85	0.38	0.31	0.06	0.01	0.59
Planktoniella muriformis (colonies)	24	24	27	32	30	12	11	26
Planktoniella sol	506	664	406	195	113	26	11	329
	0.34	0.44	0.27	0.13	0.08	0.02	0.007	0.22
Rhizosolenia spp.	24	29	64	11	6	1	1	25
Schroederella delicatula	601	456	705	220	116	47	0	364
	0.61	0.46	0.71	0.22	0.12	0.05	0	0.37
Thalassiosira rotula	442	420	969	585	57	34	0	454
	0.59	0.56	1.29	0.78	0.08	0.05	0	0.61
Σ cells/liter	7,028	7,100	7,424	3,403	1,532	352	138	4,732
Σ μg C/liter	15.51	16.59	16.98	7.17	4.37	1.04	0.77	10.67

μg C/liter, or 86% of the mean, and 3,426 cells/liter (72%).

Vertical Distribution

The mean vertical distribution of the species numerically and as carbon is given in Table 4. Selected examples of the types of vertical distribution characterizing certain species are given in Figure 2.

The standing stock declined sharply between 20 and 30 m; a uniform abundance characterized the upper 20 m. Both numerically and as biomass, the mean population at 30 m was about 45% of that at 20 m (Table 4). Expressed as carbon, and relative to the populations at 20 m, the mean populations at greater depths were only 25% (40 m), 6% (50 m) and 4.5% (75 m). About 62% of the mean carbon content of 533.5 mg C/m^2 in the upper 50 m occurred in the upper 20 m, where a mean of 16.42 μg C/liter is calculated. This pattern in vertical distribution is consistent with the mean compensation depth of about 23 m determined from Secchi disc measurements at 17 stations during this cruise leg.

The mean vertical carbon distribution of certain species (Figure 2) illustrates that peak abundance usually occurred in the upper 20 m. The phototaxic ceratians are most concentrated in the upper 10 m, with a rapid decrease (as percent of mean maximum abundance) with depth. The possibility that the "working distance" vertically within the water column varies between species is suggested by the representative distributions illustrated in Figure 2. The depth at which 50% of the mean maximum abundance occurred ranged from about 20 to 35 m between species, and from 25 to 55 m for the 25% level. Differences in light requirements, particularly that of growth at low intensities, might account for the observed distributions, if a physiological explanation can be applied. However, such distributions can also reflect differences in sinking rates, differential grazing, etc. Thus, while the underlying reasons are obscure, it is evident that the biomass distribution within and

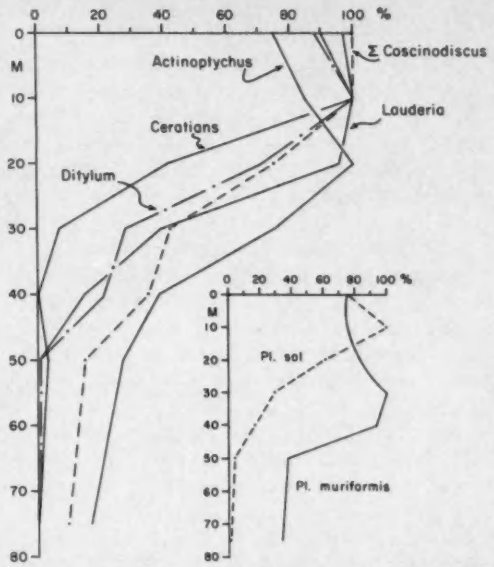

FIGURE 2.—The mean vertical distribution at all stations of *Actinoptychus undulatus*, *Ditylum brightwelli*, *Lauderia annulata*, *Planktoniella muriformis*, and *P. sol*, and for the combined *Ceratium* and *Coscinodiscus* species. Abundance is given as percent of the maximum mean abundance for each species presented in Table 4.

below the euphotic zone differs between species of phytoplankton.

BIOGEOGRAPHICAL COMMENTS

Planktoniella muriformis

Loeblich et al. (1968) described *Coenobiodiscus muriformis* as a new genus and species from north San Diego Bay, Calif., where blooms occur, and where it was reported to be in every sample collected since its first sighting in July 1966. Cultures were also established at 23° to 25°C. This unique, colonial diatom comprised up to 530 cells embedded in a one-cell thick gelatinous matrix which linked the cells in the girdle region. The circular to subcircular colonies have concave-convex shape and can be at least 500 μm in diameter. Round (1972) recently described a similar organism from the harbor at Tema in Ghana, Africa. (Environmental data were not given.) It differed from the San Diego population in the presence of considerably fewer cells per colony and slight microstructural variations. Nonetheless, Round concluded that these taxa were similar, and transferred this species to the genus *Planktoniella*.

This unique organism was conspicuous in the present survey, both in the vertical net tows and quantitative samples along the approximately 700-km track at temperatures ranging from about 11.5° to 16°C. In experiments to be described elsewhere in greater detail (Smayda in press b), the growth rate for colony increase was 2.9 and 2.0 "doublings" per day at ca. 15° to 18°C. These compare with daily colony doubling rates of 1.3 to 1.6 for cultured populations at 23° to 25°C calculated from data presented in Loeblich et al. (1968). The principal value of these data is the indication that active growth occurred under the upwelling conditions. Loeblich et al. and Round disagree as to whether all cells in the colony divide to produce a new colony, or whether growth without new colony formation can also occur.

The maximum recorded abundance of *Planktoniella muriformis* was 205 colonies/liter at the surface at Station 18. It was very common in the net tows. Thus, given its relative abundance at this time, its noteworthy appearance, and the long-term program of frequent net collections (especially during this time of year) in the coastal waters of southern and Baja California (including this survey area), carried out by Allen and Cupp, their failure to comment in any fashion on its presence is puzzling. Nor is it cited in any way in their periodic species lists for these waters (Cupp 1934; Allen 1938), or for the Gulf of California (Cupp and Allen 1938; Gilbert and Allen 1943), where floristic similarities are evident. Neither does Round (1967) mention it in his recent report on the net phytoplankton in the Gulf of California. Further, only this species and *Thalassiosira rotula*, of those found during this survey, were not found in the Gulf of Panama (Smayda 1966). Thus, the present observations suggest that *Planktoniella muriformis* is presently distributed in the Pacific Ocean from San Diego south to Punta Abreojos. But it is uncertain whether its presence and/or distribution in these coastal waters are relatively recent phenomena. Its apparent general rarity in nature and intriguing global distribution (off Baja California and Ghana) are also puzzling, although possibly an artifact of sampling. (The recent discovery of another remarkable colonial diatom, *Thalassiosira partheneia*, in the upwelling waters off Cape Blanc, Africa may also illustrate this latter problem (Schrader

1972).) It is also possible that differences in habitus account for this enigma. Loeblich et al. (1968) report that solitary cells present in cultures were unable to form colonies, and under certain conditions colonies reproduced themselves as "clusters of cells" or "a solitary pattern of growth" occurred. If the occurrence of variations in habitus correctly explains these biogeographical issues, then the factors triggering colony formation become of interest. Upwelling does not appear to be detrimental in this regard, at least during its initial stages in the survey area.

From its size, thickness, and concave-convex shape, it might a priori be presumed that *Planktoniella muriformis* is particularly well adapted for flotation and has a near-surface niche. However, the equal distribution in colony abundance in the upper 40 m is noteworthy, and contrasts to *Planktoniella sol*'s concentration in the upper 20 m (Figure 2; Table 4).

Coscinodiscus (Brenneckella) eccentricus

In the Gulf of Panama a unique centric diatom was found identified as *Brenneckella* sp. (Smayda 1966). It was characterized by an "outer, gelatinous" ring surrounding the girdle region in or on which coccolithophorids and other particulate matter were embedded. This organism was also commonplace in the present material (Tables 1, 4), and grew actively in one experiment when 2.9 divisions/day were measured (Smayda in press b). Gaarder and Hasle (1961) have reviewed its taxonomic history, the limited information on its distribution, and the potential relationships between the attached organisms and the host diatom. Based on electron microscopy, they concluded that the two species of *Brenneckella* described earlier are conspecific with *Coscinodiscus eccentricus*, a synonomy which is followed here. Nonetheless, it is listed separately as *Coscinodiscus (Brenneckella) eccentricus* in Tables 2 and 4 where mean values for the *Coscinodiscus* spp. are given.

Gaarder and Hasle suggest that the attachment of cocolithophorid cells to this diatom is a mere agglutination without any symbiotic significance. While this may be so, the relationship still remains intriguing. One may ask why other *Coscinodiscus* species, or centric diatoms, including *Planktoniella sol* characterized by an outer membrane, seemingly are invariably devoid of such epibionts.

DISCUSSION

Allen (1924, 1934, 1938) and Cupp (1930, 1934; Cupp and Allen 1938) carried out a long-term survey (approximately 1921 to 1937) of the net phytoplankton in the coastal, surface waters of southern and Baja California. These data are valuable principally in their suggestion that the net diatom community in these waters from San Diego to the Gulf of Panama is similar, inclusive of the Gulf of California (Cupp and Allen 1938; Gilbert and Allen 1943). Subsequent quantitative observations in the Gulf of Panama (Smayda 1963, 1966), net collections in the Gulf of California (Round 1967), and the present survey generally support this.

Diatoms dominated the net community (Table 4) in response to upwelling, then in its early stages. A red-tide outbreak occurred during mid-April in the survey area following a temporary subsidence of upwelling (Walsh pers. commun.). During the MESCAL I survey of 1972 in this same region the dinoflagellate *Gonyaulax polyedra* was dominant in March (Walsh et al. 1974). Its abundance then also probably reflects the occurrence of limited, if any, upwelling. Thus, annual variations in time of inception of upwelling in these waters, as well as variations within a given upwelling cycle, are reflected in the relative importance of dinoflagellates vis-à-vis that of diatoms. An abundance of diatoms will be an indication of nutrient enrichment, as is generally observed in upwelled waters.

The species composition of the diatom community is of considerable interest, given the observations of Longhurst et al. (1967). They reported that *Coscinodiscus* species, especially *C. eccentricus*, were important dominants of the upwelling communities in June and August 1964 near Magdalena Bay, lying south of the present survey area. Blooms of this genus are of exceptional interest. *Coscinodiscus*, a priori, is not generally expected to occur in great abundance pelagically in unmodified coastal and oceanic water masses. This is generally confirmed by worldwide observations, as reported in the extensive literature on phytoplankton surveys. The periodic, enormous spring blooms of *Coscinodiscus concinnus* in the North Sea are noteworthy and puzzling (Grøntved 1952).

This interest in local species composition is sustained, given the remarkable occurrence and abundance of the red crab, *Pleuroncodes planipes*,

(Longhurst 1968) in these waters. Although it is omnivorous, while herbivorous it grazes on phytoplankton cells >25 μm (Longhurst et al. 1967), i.e., the size class of *Coscinodiscus*. Indeed, these authors report active grazing on this genus under experimental conditions, and confirmed during the present study (unpubl.). Therefore, is an abundant *Coscinodiscus* community significant causally to *Pleuroncodes*, whose occurrence is a major biotic characteristic of the Baja California upwelling system? Some calculations will be made to evaluate this relationship, and to examine the other questions posed in the Introduction.

The maximum observed abundance of all *Coscinodiscus* (*Brenneckella*) spp. was 2,243 cells/liter; the mean abundance for all stations in the upper 50 m was 458 cells/liter (Table 4). This meager abundance contrasts with a mean of 4.3×10^6 cells/liter reported for *Coscinodiscus eccentricus* by Longhurst et al. (1967). In their study, this concentration represented only 8% of the total community, which was dominated by several *Nitzschia* species. *Coscinodiscus* cells of <20 μm diameter were also not present in bloom concentrations in the present material. Therefore, unlike in Magdalena Bay, this genus was not important numerically, at least during the initial stages of upwelling in the survey area.

It remains obscure whether a regional patchiness characterizes the abundance of *Coscinodiscus* during upwelling along the coast of Baja California, as for *Coscinodiscus asteromphalus* in the Gulf of California (Round 1967). Allen and Cupp referred repeatedly to such patchiness in other species in these waters. It is also possible that the *Coscinodiscus* bloom reported by Longhurst et al. represents a later state in a species succession. Finally, it might have represented an episodic bloom in response to local, unique factors, rather than reflect a general regional or successional phenomenon. Nonetheless, the reported summer abundance of *Coscinodiscus eccentricus* during upwelling in 1964 remains intriguing. The dynamics of *Coscinodiscus* populations in these waters warrant further study.

The dominant (non-setose) species numerically in the >20-μm fraction was *Lauderia annulata*, although blooms of *Schroederella delicatula* and *Thalassiosira rotula* characterized individual stations (Table 2). The total *Coscinodiscus* (*Brenneckella*) spp. represented only about 10% of the mean population numerically, but this represented 33% of the mean carbon; corresponding values for *Lauderia annulata* are 47% and 28%, respectively. Thus, although *Coscinodiscus* was not as abundant as in the Longhurst et al. survey it dominated the >20-μm biomass fraction during MESCAL II.

The percent of the total phytoplankton community represented by the >20-μm fraction can be established indirectly from chlorophyll determinations made at 10 of the stations for which quantitative >20-μm phytoplankton counts were also made. The mean concentration (based on 5 depths) in the upper 20 m was 3.46 μg Chl *a*/liter. This depth is near the compensation depth; chlorophyll determinations were not made at depths greater than this 1% level. The significant decrease in mean phytoplankton abundance between 20 and 30 m was pointed out previously (Table 4). The mean carbon content of the non-setose fraction >20 μm in the upper 20 m is 16.4 μg/liter.

Longhurst et al. (1967) give a mean carbon/chlorophyll *a* ratio of 258:1 for their material. This is exceptionally high, and contrasts with a mean (n = 17) of 110:1 characterizing the community dominated by *Gonyaulax polyedra* during the 1972 MESCAL I survey (Walsh et al. 1974). A mean ratio of 40:1 characterized diatom-dominated communities found throughout the euphotic zone in the Peru Current (Lorenzen 1968). Applying this conversion factor yields a mean carbon content of 138 μg C/liter in the upper 20 m in the present survey. If a similar carbon/chlorophyll ratio characterizes the >20-μm fraction (it may differ with cell size), then this size group (exclusive of setose species) contributes at least 12% of the viable phytoplankton carbon in the euphotic zone. *Lauderia annulata* and the *Coscinodiscus* (*Brenneckella*) species each contribute 3.5%. The non-setose component of this size grouping would appear to represent only a modest portion of the phytoplankton biomass in the euphotic zone. However, significant diel variations in this component occur, which indicate a high turnover rate. The fluxes and kinetics of this response are considered elsewhere (Smayda in press b).

Longhurst et al. (1967) estimated that the grazing rate of *Pleuroncodes* on phytoplankton was 540 liters/day per animal. Its mean abundance during MESCAL II was 1 animal/m^3 (Whitledge, pers. commun.), threefold greater than that during Longhurst and coworkers' study. The total phytoplankton population in the upper 20 m was

276 mg/m³, assuming a dry weight : carbon ratio of 2. Smith et al. (footnote 2) report a mean caloric content of 1,699 cal for *Pleuroncodes* during MESCAL II, and cite a caloric value of 3,814 cal/g dry wt for diatoms. From these data, a daily caloric ingestion of phytoplankton of 568 cal/m³ within the euphotic zone is calculated, which represents 33% of the total caloric content of the crab. *Coscinodiscus* would contribute only 1.2% of this daily caloric ingestion and the non-setose component of the >20-μm size fraction 4%, based on their contributions of 3.5 and 12%, respectively, to the phytoplankton standing stock in the upper 20 m. Even at the maximum growth rates of 3 divisions/day for *Coscinodiscus* observed during the survey (Smayda in press b) this genus would provide a negligible fraction of the daily caloric intake estimated for *Pleuroncodes*. This suggests that the *Coscinodiscus* population could not then support the *Pleuroncodes* population; other food sources were necessary.

Smith et al. (footnote 2) demonstrated that the respiration rate (as oxycaloric equivalents) of *Pleuroncodes* is only 3% of the ingestion rates calculated using the grazing rate proposed by Longhurst et al. (1967). Other calculations made by them support their notion that the grazing rate of 540 liters/day is too high, and partly accounts for the discrepancy between rates. Other factors which might contribute to the apparent feeding inefficiency of *Pleuroncodes* would be high energy losses as fecal material. Longhurst et al. observed the copious production of fecal material packed with *Coscinodiscus*. While the magnitude of this waste production during MESCAL II can not yet be evaluated, the relative rates of deposition of frustules and organic matter to the sediments when contained in fecal pellets and as free cells can be put into perspective.

The sinking rates (n = 24) of fecal pellets produced by freshly collected crabs, and determined on board ship (unpubl.), ranged from 61 to 144 m/h. These rates exceed by 1 to 4 orders of magnitude those calculated (Smayda 1970) for the different sizes of *Coscinodiscus* encountered, and that (5.2 m/hr) estimated (Smayda 1969) for the mean zooplankton fecal pellet size (320,000 μm³) collected routinely in the >20-μm fraction. Thus, while *Coscinodiscus* apparently contributed only a negligible fraction of the daily caloric ingestion of *Pleuroncodes*, the latter's ingestion and voidance in fecal material of this genus and other heavily silicified diatoms >20 μm represent a means of exceptionally rapid deposition onto the sea floor.

The mean carbon content of 138 μg/liter during the initial stages of upwelling compares with a mean standing stock of 566 μg C/liter at 20 stations reported for this region during the *Gonyaulax polyedra* bloom in March 1972 (from Table 1 in Walsh et al. 1974). The mean carbon content ranged from 23 to 100 μg/liter at three stations sampled over a 5-mo period off La Jolla, Calif. (Eppley et al. 1970). The mean concentration during upwelling south of the survey region during June 1964 ranged from 48 μg C/liter (from C/Chl a of 40:1) to 308 μg C/liter using data given by Longhurst et al. (1967). However, the data are too limited as yet for any meaningful comparison of regional or seasonal variations in apparent productivity in these coastal waters. They also indicated that the net plankton was usually more abundant in April (upwelling) between Punta Abreojos and Punta Eugenia, i.e., in the present survey area (Figure 1). However, quantitative data are needed to confirm this.

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APPENDIX TABLE 1.—List of phytoplankton taxa identified to species found in net tows and in >20-μm size fraction.

BACILLARIOPHYCEAE
- *Actinocyclus octonarius* Ehrenberg
- *Actinoptychus undulatus* (Bailey) Ralfs
- *Asterionella japonica* Castracane
- *Asterolampra marylandica* Ehrenberg
- *Asteromphalus heptactis* (Brébisson) Ralfs
- *Bacteriastrum hyalinum* Lauder
- *Biddulphia mobiliensis* Bailey
- *Biddulphia* cf. *aurita* Greville
- *Cerataulina pelagica* (Cleve) Hendey
- *Chaetoceros affinis* Lauder
- *Ch.* cf. *costatus* Pavillard
- *Ch. curvisetus* Cleve
- *Ch. debilis* Cleve
- *Ch. decipiens* Cleve
- *Ch. didymus* Ehrenberg
- *Ch. peruvianus* Brightwell
- *Ch. socialis* Lauder
- *Ch. subsecundus* (Grunow) Hustedt
- *Corethron pelagicum* Brun
- *Coscinodiscus* cf. *asteromphalus* Ehrenberg
- *C. centralis* var. *pacifica* Gran et Angst
- *C. concinnus* W. Smith
- *C. curvatulus* Grunow
- *C. eccentricus* Ehrenberg
- *C. granii* Gough
- *C. perforatus* var. *pavillardi* (Forti) Hustedt
- *C. radiatus* Ehrenberg
- *Coscinodiscus (Brenneckella) eccentricus (Lohmann)* Gaarder et Hasle
- *Ditylum brightwellii* (West) Grunow
- cf. *Ethmodiscus rex* (Rattray) Hendey
- *Eucampia cornuta* (Cleve) Grunow
- *Guinardia flaccida* (Castracane) Peragallo
- *Hemidiscus cuneiformis* Wallich
- *Lauderia annulata* Cleve
- *Leptocylindrus danicus* Cleve

BACILLARIOPHYCEAE—Cont.
- *Lithodesmium undulatum* Ehrenberg
- *Paralia sulcata* (Ehrenberg) Cleve
- *Planktoniella muriformis* (Loeblich III, Wight et Darley) Round
- *Planktoniella sol* (Wallich) Schütt
- *Rhizosolenia alata* Brightwell
- *R. bergonii* H. Peragallo
- *R. calcar avis* M Schultze
- *R. delicatula* Cleve
- *R. imbricata* var. *shrubsolei* (Cleve) Schröder
- *R. robustum* Norman
- *R. stolterfothii* H. Péragallo
- *Roperia tesselata* (Roper) Grunow
- *Shroederella delicatula* (Peragallo) Pavillard
- *Skeletonema costatum* (Greville) Cleve
- *Stephanopyxis turris* (Greville) Ralfs
- *Thalassionema nitzschioides* (Grunow) Hustedt
- *Thalassiosira rotula* Meunier
- *Thalassiothrix frauenfeldii* Grunow
- *T. longissima* Cleve et Grunow
- *T. mediterranea* var. *pacifica* Cupp

DINOPHYCEAE
- *Ceratium furca* (Ehrenberg) Claparede et Lachmann
- *Ceratium fusus* (Ehrenberg) Dujardin
- *Dinophysis miles* Cleve
- *Gonyaulax* cf. *polyedra* Stein
- *Noctiluca scintillans* (Macartney) Kofoid et Swezy
- *Pyrocystis* cf. *lunula* Schütt
- *Pyrophacus horologicum* Stein

CHRYSOPHYCEAE
- *Distephanus speculum* (Ehrenberg) Haeckel

HAPTOPHYCEAE
- *Phaeocystis poucheti* (Hariot) Lagerheim

PRASINOPHYCEAE
- cf. *Halosphaera viridis* Schmitz

OPTIMUM ECONOMIC YIELD OF AN INTERNATIONALLY UTILIZED COMMON PROPERTY RESOURCE[1]

LEE G. ANDERSON[2]

ABSTRACT

The exploitation of a common property resource, specifically a fishery, by nationals of two countries is discussed using a simple general equilibrium analysis. The interdependence of their production possibility curves is used to describe the open-access equilibrium yield, local maximum economic yields, and a true international maximum economic yield. Finally a complete description of the conditions necessary for this international maximum economic yield and why they are different from those in a national fishery is presented.

The purpose of this paper is to analyse, using a simple general equilibrium model, the problem of the allocation of resources where common property or open access exists for some of them. The common property or open-access resource will be a fish stock. The economics of fisheries has been quite extensively developed. See for example Gordon (1954), Scott (1955), Crutchfield and Zellner (1962), Turvey (1964), Crutchfield (1965), Christy and Scott (1965), Smith (1969), Copes (1970), Scott and Southey (1970), Gould (1972), Southey (1972), and Anderson (1973). The present paper follows Scott and Southey and uses a production possibility (PP) curve model which takes into direct account all the resources of the economy and not just the fishery. This change in focus is especially useful for analysing economic aspects of international use of common property resources, a problem that has long been recognized but which has received very little treatment to date. The following quote from Christy and Scott (1965:223) summarizes the problem fairly well:

> "Two countries contemplating the same fishery may rightly make different choices about the intensity and combination of fishing activities .... These different valuations are ultimately the result of the obstacles to the movement of factors from one economy to another. More directly, they result from differences in population, national income, and tastes. It is a commonplace of the theory of comparative costs that the same industry may use a different technique in each country, depending on the structure of wages and prices in each place. But it has never, to our knowledge, been pointed out that the ocean is the main locale where these structures clash .... Of course, it is possible to exaggerate these discrepancies. Forces outside the fisheries tend to bring the national wage and price structure into line, through the movement of goods and the sale of services. And within the fishery itself the increasing international trade in this equipment, all tend to press toward a uniform set of labor-capital-fish price-ratios."

The model presented will allow a more formal analysis of these and other problems.

The first section of the paper describes a one country model of the economics of fisheries from a general equilibrium point of view. Results identical to the earlier works are derived as a starting point for discussion. The second section expands the model to consider two nations both having access to the same fish stock and describes the conditions necessary for an international open-access equilibrium yield, for local maximum economic yields (MEY), and for a true international MEY. The third section describes the conditions for an international MEY in more detail and shows the ways in which the countries can go about achieving them. Throughout the analysis is static.

I

Consider a country with a specified amount of resources, a given technology, and exclusive use (either through default or international law) of a fish stock. Using its resources, it can either produce manufactured goods (M) or fishing effort (E) which can be applied to the fish stock to catch fish. Let the implicit function for the PP curve between M and E be:

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$$G(E, M) = 0. \quad (1)$$

Assume that it is quasi-concave so that there will be a concave transformation curve between E and M. Let the sustained yield curve of the fish stock (i.e. the production function) be expressed as:[3]

$$F(E) = aE - bE^2. \quad (2)$$

Using this equation assumes that the fish stock will always be in a biologic equilibrium. F will increase until E is equal to $\frac{a}{2b}$ and will thereafter decrease. F will be zero when $E = 0$ and when $E = \frac{a}{b}$. As long as the maximum amount of E possible is greater than $\frac{a}{2b}$ but less than $\frac{a}{b}$, then the PP curve for M and F will be similar to the solid one in Figure 1. (Ignore for the moment the dotted one.) The slope of the curve is:

$$\frac{dF}{dM} = \frac{dF}{dE}\,\frac{dE}{dM} = -(a - 2bE)\,\frac{G_2}{G_1} \quad (3)$$

where G_1 is the derivative of G with respect to its first argument, etc. Fish output will be at a maximum when E equals $\frac{a}{2b}$, not when all of the resources are used in the production of E. As long as the marginal productivity of E in fishing is negative, the PP curve will have a positive slope. Switching resources out of effort and into manufacturing will actually increase both F and M. Where E's marginal productivity in F is positive, the PP curve will have its normal negative slope. Because both $\frac{G_2}{G_1}$ and $(a - 2bE)$ increase as M increases (i.e. as E decreases), the curve will be concave to the origin. Also assume that there is a linearly homogeneous social utility function of the form

$$U = U(F, M). \quad (4)$$

As pointed out in the literature cited above (see especially Turvey 1964 and Scott and Southey 1970), as long as no one regulates entry into the fishing industry, profit maximizing individuals will continue to produce or buy E as long as the value of the average catch per unit of E is greater than the price of effort. The effects of this are as follows. If E and M are produced in pure competition, then $-\frac{P_M}{P_E} = \frac{dE}{dM}$. Equilibrium will occur in the open-access fishery when $P_F\frac{F}{E}$ equals P_E; that is when the average return to effort equals its cost. [Smith (1969) has shown that under certain circumstances, the fishery will not reach an equilibrium. For the moment let us ignore this possibility although its effects will be discussed briefly below.] It can be shown therefore that with an open-access fishery and pure competition in the production of E and M, producers will arrange their production such that for any given price ratio the following condition will hold:

$$-\frac{P_M}{P_F} = \frac{F/E}{dM/dE}. \quad (5)$$

Maximum consumer welfare occurs where the slope of the social indifference curve is equal to the price ratio. That is where

$$-\frac{U_2}{U_1} = -\frac{P_M}{P_F}.$$

Therefore a general equilibrium in the production and the consumption sectors of the economy will occur when

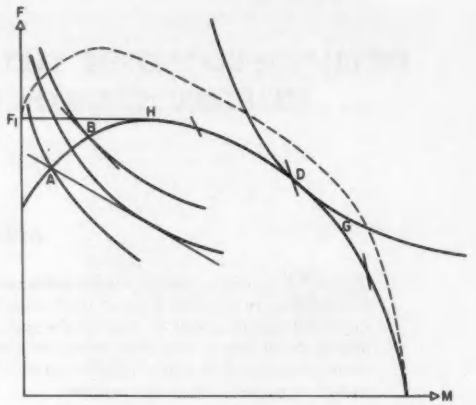

FIGURE 1.—The solid concave curve is the production possibility curve and the set of convex curves are the community indifference curves. Open-access equilibrium will occur at B, maximum sustainable yield at H, and maximum economic yield at D. In the two country model, a decrease in fishing effort in the other country will shift the production possibility curve to the dotted one.

[3]The sustained yield curve is the relationship between the amount of effort expended and the amount of fish that will be captured period after period. The particular expression here follows Schaefer (1957). Although other expressions have been discussed recently (see the papers by Southey and Gould cited above), Expression (1) is descriptive enough to capture the essentials of the argument.

$$-\frac{U_2}{U_1} = -\frac{P_M}{P_F} = \frac{F/E}{dM/dE} . \qquad (6)$$

Conditions for the maximization of social welfare, however, are:

$$-\frac{U_2}{U_1} = -\frac{P_M}{P_F} = \left[\frac{dF/dE}{dM/dE} \equiv \frac{dF}{dM}\right] . \qquad (7)$$

An expression for $\frac{dF}{dM}$ is given in (3) and $(F/E)/(dM/dE)$ can be expressed as:

$$(F/E)/(dM/dE) = -(a - bE)\frac{G_2}{G_1} . \qquad (8)$$

The ratio $\frac{F/E}{dM/dE}$ will increase in absolute size as M increases, and because of the assumption that the maximum E is less than a/b, it will always be negative, even when the slope of the PP curve is positive. It can be seen that when they are both negative, this ratio will be larger in absolute size than the slope of the PP curve at that point; i.e. it will have a steeper slope. The small lines on the PP curve in Figure 1 represent the ratio $\frac{F/E}{dM/dE}$ at that point.

In terms of Figure 1, open-access equilibrium will occur at point B where the slope of the indifference curve as it intersects the PP curve is equal to the ratio of $\frac{F/E}{dM/dE}$ at that point.[4] The social optimum is at point D where the indifference curve is just tangent to the PP curve. The common property or open-access equilibrium will always be to the left of the optimal point; therefore with open access, too many resources will be allocated to F under the market system. It is even possible that the market equilibrium will occur in the positive sloped segment of the PP curve.

By way of comparing the present analysis with the standard one, point H on Figure 1 is the point of maximum sustained yield for a fishery and point D is the MEY. The latter point has less fish but more manufactured goods than the former (and may even have less fish than the point where the unregulated fishery will operate). At MEY, however, no fish is produced unless its value is greater than its opportunity cost. Although MEY in the traditional literature refers to a specified amount of fish production, it assumes that the resources not in fishing are used efficiently in the production of other goods. Describing the model in terms of a PP curve makes this explicit.

Through proper regulation, the country can move to MEY. This could involve a ceiling on the amount of fishing effort allowed or the granting of property rights to the fishery to certain individuals. The former has been tried but usually by means of decreasing efficiency rather than by shifting resources to other types of production, and the latter can lead to monopoly or oligopoly unless the property rights are distributed widely or there are other fish stocks that can provide the necessary competition.

If the government only allows α units of effort, where α is less than the open-access amount of effort, and then distributes the rights to this number of units among a large enough group such that there is still pure competition in the market for both effort and fish, these people will be earning a rent per period, R, of $P_F F(\alpha) - P_E \alpha$ where $F(\alpha)$ is the amount of fish caught by α units of effort. Unless reductions in effort have perverse effects on price, average catch, or cost of effort, this rent will be positive. See Anderson (1973:513).

The optimal amount of effort is where the total amount of rent is a maximum (Christy and Scott 1965:8). By using the standard mathematical procedure it can be shown that the first order condition for R to be a maximum is:

$$P_F \frac{dF}{dE} = P_E .$$

Under the above assumptions, the open-access problem of the fishery has been solved in a way that keeps pure competition in the production of M and E. Therefore $-P_M/P_E$ is equal to dE/dM and so maximization of the rent of the fishery will guarantee that

$$-\frac{P_M}{P_F} = \frac{dF/dE}{dM/dE} = \frac{dF}{dM} \qquad (9)$$

This will mean that the conditions for the maximization of social welfare, expressed in (7) above, will hold. Therefore a policy that maximizes the rent from the fishery also maximizes social welfare.

In summary, a country with exclusive rights to an open-access fishery will operate inefficiently as

[4] As Scott and Southey (1970) point out, if there are increasing returns to scale and if the social utility function is not linearly homogeneous, it is possible that there may be multiple equilibria. I have ignored that complication for purposes of this paper.

long as there is no regulation of fishing effort. This will be because as long as the average returns to fishing are greater than the price of effort, private decision makers will continue to demand E. Also since E and F are directly related, there is always a direct relationship between P_E and P_F.

II

Now to turn to the case of more than one country exploiting the same fish stock, analysis of this is made very difficult by a variety of intriguing problems. For instance, technology may be so different in the two countries that it is very hard to find a common measure of fishing effort, tastes may be such that one country prefers small fish while the other prefers large ones and yet the sustained yield curve is dependent on the size of catch, each country may be using other criteria for harvesting the fish; for example, one may look at it as a place to put unemployed labor, or as a source of earning foreign exchange. For purposes of discussion these intricacies will not be considered.

Assume that two countries, country X and country Y, both with specified production capacities ($G^X(E_X, M_X) = 0$ and $G^Y(E_Y, M_Y) = 0$) and linearly homogeneous community welfare functions ($U^X = U^X(F_X, M_X)$ and $U^Y = U^Y(F_Y, M_Y)$, are the exclusive users of a fish stock with the sustainable yield curve (2) above. Since a unit of effort in country X, (E_X), is identical to one in Y, (E_Y), the sustained yield curve can be expressed as:

$$F(E_Y, E_X) = a(E_X + E_Y) - b(E_X + E_Y)^2.$$

As before the total catch from the fishery will reach a maximum when E_X plus E_Y is equal to $\frac{a}{2b}$ and will fall to zero if total effort gets as large as $\frac{a}{b}$.

The catch of one country will be in proportion to its effort in relation to total effort, therefore:

$$F_X(E_X, E_X) = \frac{E_X}{E_X + E_Y}\left[a(E_X + E_Y) - b(E_X + E_Y)^2\right].$$

This can be simplified to:

$$F_X = aE_X - bE_X^2 - bE_XE_Y. \qquad (10)$$

F_X will reach a maximum when E_X equals $\frac{a - bE_Y}{2b}$ and will fall to zero if it gets as large as $\frac{a - bE_Y}{b}$. The equation for F_Y is analogous.

The amount of fish that country X can catch using a specified amount of E_X depends upon how much E_Y country Y is producing and using. Similarly the catch of country Y depends upon the amount of E_X used by country X. Therefore, the shape and position of each country's PP curve for F and M is dependent upon the amount of E the other country uses. Let the two PP curves in Figure 1 be two possible ones for country X. The solid one is for the larger level of E_Y. Note that the lower curve gets further away from the higher one as M_X decreases. This is because $\frac{\partial F_X}{\partial E_Y}$, the vertical displacement of the curve due to a change in effort in country Y, is equal to $-bE_X$. Therefore, the higher the level of E_X, that is the lower the level of M_X, the greater will be the vertical displacement. The maximum amount of F_X will be at a higher amount of M_X (a lower amount of E_X) because F_X is a maximum when E_X is equal to $\frac{a - bE_Y}{2b}$.

Using this two country model let us consider the implications of three types of exploitation: 1) open access in both countries, 2) local MEY in both countries, and 3) a true international MEY.

From the above description, it can be seen that the shape and position of the PP curve for M and F in each country is dependent upon the level of effort used in the other. Therefore the open-access free market equilibrium in each country will depend upon the level of effort used in the other. The mathematical condition for an international open-access equilibrium is the following set of simultaneous equations:

$$\text{Country } X \quad \frac{U_2^X}{U_1^X} = \frac{F_X/E_X}{dM_X/dE_X} \qquad (11a)$$

$$\text{Country } Y \quad \frac{U_2^Y}{U_1^Y} = \frac{F_Y/E_Y}{dM_Y/dE_Y}. \qquad (11b)$$

This simply states that the open-access condition for each country (see Equation (6)) must hold in both simultaneously. In terms of Figure 1, each country must be operating at a point such as B.

Note however, that in country X, average catch (F_X/E_X) is a function of both E_X and E_Y. Therefore an equilibrium in country X can be reached only for a given level of E_Y, (i.e. for a given PP curve). Similarly an equilibrium in country Y is possible only for a given level of E_X. Therefore an international equilibrium is possible only at that combination(s) of E_X and E_Y where Equations (11a) and (11b) both hold simultaneously.

If free international trade between these countries is possible, the price ratios in both countries will be equalized, and so at the equilibrium, the marginal rates of substitution $\left(\frac{U_2}{U_1}\right)$ will also be equal. Therefore the following condition will hold:

$$\frac{U_2^X}{U_1^X} = \frac{U_2^Y}{U_1^Y} = \frac{F_X/E_X}{dM_X/dE_X} = \frac{F_Y/E_Y}{dM_Y/dE_Y}. \quad (12)$$

Graphically the international trade case can be interpreted as follows. For a given level of E produced in the other country, each country will produce at that point on the PP curve where the trade price ratio is equal to $\frac{F/E}{dM/dE}$. It will then trade along the price ratio line until welfare is maximized. Consider a country that would operate under autarky at point B in Figure 1. Under our assumptions the location of the PP curve is related to the amount of E being produced in the other country. If trade opens up with a lower $\frac{P_M}{P_F}$, the production point will move to A, but the consumption point will be at C because of imports of M and exports of F. From this it can be concluded that for each level of E produced in the other country, a decrease in $\frac{P_M}{P_F}$, i.e. a relative increase in P_F, will increase the amount of E produced locally.

As a sidelight notice that the decrease in $\frac{P_M}{P_F}$ actually decreased the welfare of the fish exporting country described in Figure 1. Trade allowed for a further misallocation of resources due to an expanding market for fish to such an extent that welfare fell. Of course, if the price line through A intersected the indifference curve through B, then welfare would have been increased in spite of the harmful effects. To be precise it should be noted that in the general equilibrium analysis, the amount of E produced by the other country will fall in most cases which will shift the PP curve out and may cause welfare to increase enough to overcome the initial loss. On the other hand, increases in $\frac{P_M}{P_F}$ brought about by trade will improve the allocation of resources and always increase welfare initially; however, the increase in E in the other country will have the opposite effect on welfare. So whether the country exports or imports fish, changes in the terms of trade may decrease welfare depending upon the direction and magnitudes of the changes caused by these two factors.

Equation (7) above states the condition for the maximization of social welfare (i.e. MEY) in the one country case. With free international trade, if both countries attempt to maximize welfare given the level of effort used in the other country, the condition for an international equilibrium is:

$$\frac{U_2^X}{U_1^X} = \frac{U_2^Y}{U_1^Y} = \frac{\partial F_X/\partial E_X}{dM_X/dE_X} = \frac{\partial F_Y/\partial E_Y}{dM_Y/dE_Y}. \quad (13)$$

The last two terms can be simplified to $\frac{\partial F_X}{\partial M_X}$ and $\frac{\partial F_Y}{\partial M_Y}$ respectively. These will be recognized as the slopes of the PP curves of the two countries. What this condition states is that for a local MEY, the marginal rate of substitution between M and F in each country must equal each other and they must also equal the internal marginal rate of transformation between M and F given the level of effort in the other country. In terms of Figure 1, each country will be operating at a point such as D, where the slope of the social indifference curve is equal to the slope of the existing PP curve. Notice that in equation (13), $\frac{\partial F_X}{\partial E_X}$ and $\frac{\partial F_Y}{\partial E_Y}$ are both partially determined by the level of effort in the other country, so that here again the equilibrium combination of E_X and E_Y must be simultaneously determined.

One main purpose of this paper is to describe the necessary condition for an international MEY. It is important to note at this time that they are different from Equation (13), the conditions of local MEY's given the level of effort in the other country. Since the level of effort in each country affects the PP curve, and hence potential welfare, in both countries, the maximizing conditions

must take this into account. With free international trade, these conditions are:[5]

$$-\frac{U_2^X}{U_1^X}=\frac{U_2^Y}{U_1^Y}=\frac{\frac{\partial F_X}{\partial E_X}+\frac{\partial F_Y}{\partial E_X}}{\frac{dM_X}{dE_X}}=\frac{\frac{\partial F_Y}{\partial E_Y}+\frac{\partial F_X}{\partial E_Y}}{\frac{dM_Y}{dE_Y}}. \quad (14)$$

Alternatively this condition can be written as:

$$-\frac{U_2^X}{U_1^X}=-\frac{U_2^Y}{U_1^Y}=\frac{\overset{(-)}{\partial F_X}}{\partial M_X}+\frac{\overset{(+)}{\partial F_Y}}{\partial M_X}=\frac{\overset{(-)}{\partial F_Y}}{\partial M_Y}+\frac{\overset{(+)}{\partial F_X}}{\partial M_Y}. \quad (14')$$

Expression (14) is useful for comparisons with the open-access free market international equilibrium conditions in (12) and with the local MEY condition in (13), while Expression (14′) is useful for tying the analysis to the PP curve.

In words these conditions state that the marginal rate of substitution for M and F and a special type of marginal rate of transformation (MRT) in both countries must equal each other. The marginal rate of transformation is special in that it considers the effect on fish production in both countries, of a change in manufacturing in only one. To be more precise a "socially optimal" international policy should guarantee that neither country expand their fishing effort unless the value of the extra yield, regardless of who catches it, is equal to the value of the extra M that must be foregone. That is country X should compare the opportunity value of producing effort with its effect on local catch $(\frac{\partial F_X}{\partial M_X})$ and with its effect on country Y's catch $(\frac{\partial F_Y}{\partial M_X})$. The same restriction must be placed on country Y's fishing industry also.

It is important to stress at this point that these international MEY conditions were derived by maximizing the level of welfare in one country while specifying a certain level in the other. That is, an initial distribution of the fishery is essential before the maximizing conditions for an international MEY can be utilized. This same condition will hold at many combinations of E_X and E_Y depending upon how the wealth of fishery is distributed. This is one of the major differences between a national MEY and an international MEY. The importance of the beginning distribution will be discussed in greater detail in Section III.

It can be shown from the equations for F_X and F_Y that $\frac{\partial F_X}{\partial E_X}+\frac{\partial F_Y}{\partial E_X}$ equals $\frac{\partial F_Y}{\partial E_Y}+\frac{\partial F_X}{\partial E_Y}$ and that F_X/E_X equals F_Y/E_Y. Therefore in both the open-access equilibrium (Condition 12) and at any true international optimum point (Condition 14), dM_X/dE_X must equal dM_Y/dE_Y. That is, the real cost of producing fishing effort will be the same in both countries. The difference is that only in the

[5]This condition can be derived in the following manner. With international trade, the community welfare functions become

$U^X = U^X\ [F_X(E_X, E_Y) + F_T, M_X + M_T]$ and

$U^Y = U^Y\ [F_Y(E_Y, E_X) - F_T, M_Y - M_T]$

where F_T and M_T are the amounts of F and M respectively that are traded. If we wish to maximize the welfare of country X subject to a specified amount in country Y and to the productive capacities, we get the following Lagrangian function.

$$L = U^X + \lambda_1(U^Y - \bar{U}^Y) + \lambda_2 G^X(E_X, M_X) + \lambda_3 G^Y(E_Y, M_Y).$$

The first order conditions for a maximum (using the normal notation for derivatives) are:

(a) $\frac{\partial L}{\partial E_X} = U_1^X \frac{\partial F_X}{\partial E_X} + \lambda_1 U_1^Y \frac{\partial F_Y}{\partial E_X} + \lambda_2 G_1^X = 0$

(b) $\frac{\partial L}{\partial M_X} = U_2^X + \lambda_2 G_2^X = 0$

(c) $\frac{\partial L}{\partial E_Y} = U_1^X \frac{\partial F_X}{\partial E_Y} + \lambda_1 U_1^Y \frac{\partial F_Y}{\partial E_Y} + \lambda_3 G_1^Y = 0$

(d) $\frac{\partial L}{\partial M_Y} = \lambda_1 U_2^Y + \lambda_3 G_2^Y = 0$

(e) $\frac{\partial L}{\partial M_T} = U_1^X + \lambda_1 U_1^Y = 0$

(f) $\frac{\partial L}{\partial F_T} = U_2^X + \lambda_1 U_2^Y = 0.$

Note that Conditions (a) and (c) show that a change in the level of effort in one country has a direct effect on the level of welfare on the other. For this reason the Pareto conditions for an international optimum are different than in the standard case. Solving (e) for λ_1 substituting that expression in (a) and then dividing (b) by (a) yields

$$-\frac{U_2^X}{U_1^X}=\frac{\frac{\partial F_X}{\partial E_X}+\frac{\partial F_Y}{\partial E_X}}{-\frac{G_1^X}{G_2^X}}.$$

Similarly substituting the value of λ_1 into (c) and (d) and then dividing (d) by (c) yields

$$-\frac{U_2^X}{U_1^X}=\frac{\frac{\partial F_Y}{\partial E_Y}+\frac{\partial F_X}{\partial E_Y}}{-\frac{G_1^Y}{G_2^Y}}.$$

Since from (e) and (f) it can be shown that $-\frac{U_2^X}{U_1^X}=-\frac{U_2^Y}{U_1^Y}$, and by definition $-\frac{G_1^X}{G_2^X}=\frac{dM_X}{dE_X}$ and $-\frac{G_1^Y}{G_2^Y}=\frac{dM_Y}{dE_Y}$, it can be shown that Condition (12) holds.

latter is the proper amount of it produced. The equalizing mechanism in both cases is the trade in fish which is indirect trade in effort.

Figure 2 depicts the international MEY situation in terms of the PP curve of both countries. Expression (14′) says that the absolute value of the slope of the indifference curves in both countries ($-\frac{U_2}{U_1}$) must be less than the absolute value of the slope of their existing PP curves at the point of operation ($\frac{\partial F}{\partial M}$). That is at the equilibrium point, the slope of the indifference curve must be less steep than the slope of the PP curve. Therefore the slope of the price ratio line must also be less steep than the slope of the PP curve. What this means is that both countries must produce less fish than they would under normal free market conditions given the relative cost of producing F and M. The reason for this is that they must take into account the effect of their output levels on the production of fish in the other country. In the diagram the regulated price ratio common to both countries is represented by the two straight lines. Country X, producing at point A and consuming at point B, is importing M_T units of M and exporting F_T units of F. Country Y, producing at point A′ and consuming at point B′, is doing the reverse. Since at the equilibrium, producers in both countries are basing the production decision on the same price ratio, and since $\frac{dM_X}{dE_X} = \frac{dM_Y}{dE_Y}$, there will be no balance of payments problem; i.e. the value of F traded will equal the value of M traded.

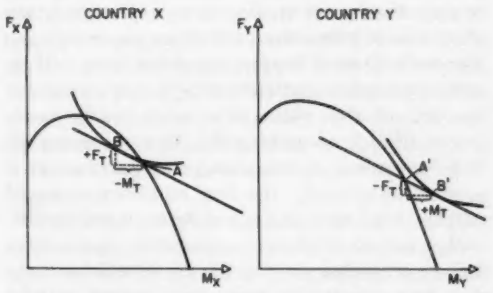

FIGURE 2.—In the two country case, the international maximum economic yield can be represented by the countries producing at A and A′ and consuming at B and B′, the difference being made up by international trade. The exact relationship between the slope of the indifference curves and the production possibility curves is expressed in Equations (14) and (14′).

Two technical points regarding this diagram should be pointed out. First, since there are international interdependencies involved, operation at the international MEY requires government regulation. Some form of taxes or other means of control will be necessary in each country to keep producers operating where the price ratio to consumers, as represented by the slope of the indifference curve, is different than the ratio of marginal costs of production, as represented by the slope of the PP curve. Second, it may seem strange that country X, the importer of fish, is consuming at a point inside its existing PP curve. (If the indifference curve for country Y through point B′ intersects the PP curve, that country will also be operating at a point where its welfare is not as large as it might be given its existing PP curve.) Would it not be to its advantage to stop trading and expand its own fishing by moving up its PP curve? In answering this question it must be remembered that the only reason country X's PP curve is as high as it is, is that country Y has reduced its level of effort. Only if country Y were foolish enough to keep its level of effort the same regardless of country X's behavior would the latter benefit from an increase in effort. It would gain welfare while country Y would lose. This discussion points out, however, that proper management of international fisheries will be difficult to enforce because one or both of the countries involved will be motivated to increase effort from the optimal point.

So far three distinguishable points on each PP curve can be identified: the open-access equilibrium point (where the slope of the indifference curve, or the international price line, as it intersects the PP curve equals $\frac{F/E}{dM/dE}$, i.e. point B in Figure 1); the local MEY optima given the level of effort in the other country (where the slope of the indifference curve or the international price line is equal to $\frac{\partial F}{\partial M}$, i.e. point D in Figure 1); and the point where the country contributes to an international MEY given the level of E produced abroad, i.e. at point A or A′ in Figure 2. With regard to the latter, only if both countries are operating in this fashion, is it a true international MEY, where the value of the net increase in fish production by the marginal unit of effort, regardless of its origin,

is just equal to the value of the resultant decrease in the production of M.

As a sidelight it is interesting to note that if one country unilaterally adopts a local optimum regulation policy given the level of effort in the other country, at the new equilibrium it will be using less effort and in most cases the other country will react to this by increasing their level of effort. Therefore, while the decrease in effort will increase its level of welfare (it will move from point B to point D in Figure 1), the increase in effort by the other country will shift the PP curve toward the origin, and this will reduce the gains. It is even possible that the shift of the PP curve could be large enough that at the new equilibrium the country actually loses welfare.

This has interesting implications for cases where international cooperation in fisheries management does not exist. National regulation policies must be derived taking into account the reaction of other countries to specific actions. Each country will have to know how the other will react to a change in its level of effort. Taking this into account, it should only reduce its own effort (i.e. transfer resources from producing effort into the production of M) as long as the resultant increase in welfare is greater than the decline due to any possible increase in foreign fishing.[6] If these reactions are not known, the determination of the proper regulation program will require some sort of game theory approach.

In conclusion it should be pointed out that simply because it is possible to list the conditions that are necessary for a certain type of equilibrium to exist does not mean that it will in fact exist. As Smith (1969) has pointed out, a fishery will reach a bionomic equilibrium only if certain relationships exist between the growth rate of the fish stock and the rate at which effort enters and leaves the fishery (either because of market forces or regulatory decree). As pointed out earlier, however, the present analysis is static and will ignore these complications.

III

It will prove useful to view the problem from a different angle. There are two countries each with its own productive capacity and preference function, and between them they share an open-access fishery. Given this information, it is possible to construct a welfare possibility curve for the two countries (Figure 3). Any point on the curve is the maximum amount of welfare that can be obtained for one country at the level of welfare specified for the other country given the productive capacities of both countries and the sustained yield curve of the fishery. At any point on the curve, Condition (14) holds. Therefore, at each point there is an international MEY from the fishery since in all cases the value of the last fish caught will be worth its opportunity cost. As is well known, there is no way of choosing one point on the curve from another.

To digress a moment, if there were no open-access resources or other market imperfections, the two countries through market-directed production and trade will end up at a point on that possibility curve. If they each operated independently, they could obtain a certain amount of welfare, say the amounts represented by point A. Under free market conditions, each would be motivated to change its output combination and then trade such that both would be better off at a point such as B. Point B is not inherently superior to any other point on the curve. It is merely the point where given the productive capacities and the preferences of the two countries, they will operate under the conditions of a free international market. At that point no country can be made better off without making the other one worse off. If for some reason there was a redistribution of productive capacity, the final equilibrium would still be on the curve but at a different point than B.

Now to turn back to the case of the open-access fishery, if neither country exploits the fishery and they do not engage in trade, then operating independently, each would be able to obtain a certain amount of welfare. Again let this point be represented by A in Figure 3. If free trade is introduced and if both countries begin to exploit the fishery taking into account the effect of their effort

[6] In formal mathematical terms the country must maximize welfare subject to its production constraint knowing that the equilibrium level of effort in the other country is a function of its own effort. The proper Lagrangian for country X and its first order conditions are:

$$L_1 = U^X[F_X(E_X, E_Y(E_X)), M_X] + \lambda_1 G^X(E_X, M_X)$$

$$\frac{\partial L_1}{\partial E_X} = U_1^X\left[\frac{\partial F_X}{\partial E_X} + \frac{\partial F_X}{\partial E_Y}\frac{dE_Y}{dE_X}\right] + \lambda_1 G_1^X = 0$$

$$\frac{\partial L_1}{\partial M_X} = U_2^X + \lambda_1 G_2^X = 0.$$

The first order condition with respect to E_X takes into account the total effect on the amount of fish caught by a change in effort. There is the direct change in catch and the indirect effect caused by a change in the level of effort in country Y.

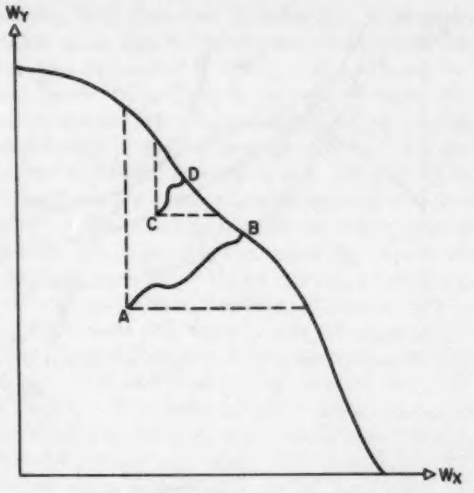

FIGURE 3.—Each point on the curve represents a distribution of the fishery where one country cannot be made better off without hurting the other. B represents the point where it is distributed on the basis of ability to harvest fish. C represents the distribution that is obtained by open-access exploitation. While both countries can benefit from changes from this point, note that in this case a move to the "ability" distribution at B represents a decrease in the welfare of country Y.

on the catch in the other country, a point such as B on the possibility curve will be reached. The wealth from the fishery will have been distributed between the two countries on their ability to produce the effort to harvest it. In fact, if the cost of effort was always less in one country, then at the MEY point, that country would be doing all the fishing and gaining all the wealth from the fish stock. The other country would gain from trade in goods but not from the fishery itself. There is nothing inherently superior about point B, however. There does not appear to be a moral argument that one country deserves the wealth from an international common property resource simply because it has a comparative advantage in the ability to capture it.

Under open-access conditions, the two countries will operate somewhere inside the welfare possibility curve, say at point C. This point is analogous to the solution of Equations (11a) and (11b). It is possible for both countries to increase their welfare by moving to a point such as D. Just how these gains can be obtained is discussed in detail below. But for now notice that in the case depicted here, if the countries are forced to move to point B (i.e. the point where the wealth from the fishery is distributed on the basis of ability to produce effort), country Y will suffer a decrease in welfare. This will not always be the case but will depend upon the position of C relative to that of B.

The point to be made from all this is that distribution is a critical part of determining the makeup on an international MEY. It is important to separate who obtains the wealth from the fishery from who harvests the fish. When the two are linked together, economic efficiency can be obtained only if the fishery is distributed according to ability to harvest. Under these conditions, therefore, one of the countries may suffer a decrease in welfare in the process of obtaining an international MEY. However if distribution and harvesting can be separated, an international MEY can be obtained using any criterion for distribution. Further, one can be obtained whereby both countries will improve their welfare from that at the open-access equilibrium.

The remainder of this paper will discuss a process for reaching an international MEY making explicit the distributional problem and its relationship with Condition (14). Let us consider how two countries that are operating at a point such as C in Figure 3 can move to an international MEY at a point such as D. Such a move would entail up to four mutually inderdependent types of trades between the two countries, including trade in mutual changes in fishing effort (essentially trades that alter, to the mutual advantage of both countries, the property rights to the fishery from those established by the rule of capture in the open-access fishery), trade in fishing effort or rights to fish when one country has the right to fish but the other can produce effort with less cost, and trade in the produced goods F and M. The first of these trades establishes a distribution of the fishery, and the rest insure that Condition (14) will hold for that distribution. These trades are interdependent since any trade can alter demand conditions if the gains are large relative to wealth. Each of these trades will be discussed separately so as to clarify the concepts involved. It should be remembered however, that the theoretical maximum advantage from international cooperation can not be achieved unless the trades are considered simultaneously.

First let us consider the potential for mutual gain from trade in mutual changes in fishing effort. Assume that two countries have reached an international open-access equilibrium with coun-

try X producing E_{X1} units of effort and country Y producing E_{Y1} units. (To be completely general this combination of effort can also be thought of as the one that both countries agree to use as an initial bargaining point.) Assume that under these conditions country X is operating at point A in Figure 4a. At that point, which is on social indifference curve I_1, there is a specified amount of E_Y (which determines the shape and position of X's PP curve) and E_X (which determines the position on the curve) being produced. There are other combinations of E_X and E_Y that will cause X to operate on I_1 however. For example, if E_Y remains the same and E_X is reduced (i.e. resources are shifted from the production of effort to manufacturing) such that there is a movement to point B, the level of social welfare will not change.[7] Smaller reductions of E_X that are matched by increases in E_Y will leave welfare unchanged if the increase in E_Y shifts the PP curve down such that the country is still operating on I_1. Similarly, increases in E_X, or reductions by more than is necessary to shift the country to point B, will result in constant welfare if there is a simultaneous reduction in E_Y large enough to shift the PP curve up by the appropriate amount.

This information can be more meaningfully displayed in terms of the property right indifference curves (PRI curves) in Figure 4b. The axis represent allowable levels of E_X and E_Y. These allowable levels are essentially property rights to the annual harvest that the specified amount of E will catch. They are labeled PR_X and PR_Y, but when there is no trade in effort, then E_X equals PR_X and E_Y equals PR_Y. Point A′ represents the international open-access equilibrium point. That is, E_{Y1} is the level of effort in country Y that will cause country X to be operating on the PP curve in Figure 4a, and E_{X1} is the amount of effort in country X that will cause it to operate at point A on that curve. Every other point in the diagram represents a different combination of effort in each country and, in effect, represents a distribution of the fishery. Point A′ is the distribution of the property rights by the rule of capture. Movements to the left represent reductions in the amount of allowable effort for country X, and downward

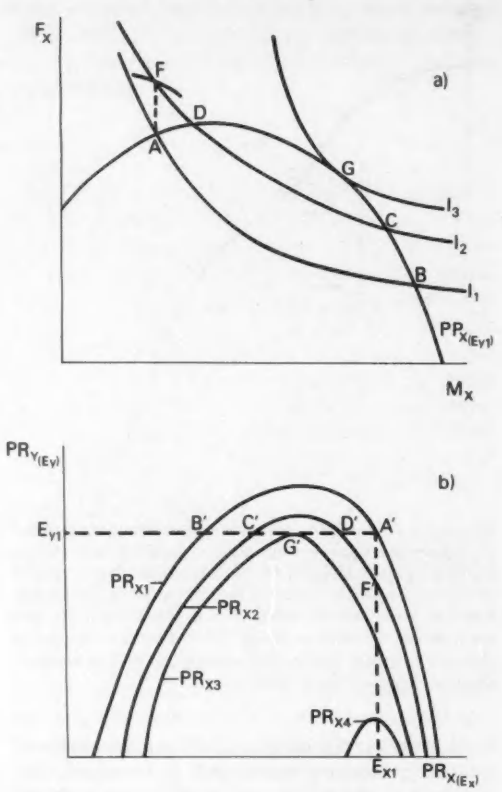

FIGURE 4.—The property right indifference (PRI) curves for each country follow directly from the relationship between their production possibility curves and indifference curves.

movements represent a reduction for country Y. PRI_{X1} is that collection of bundles of PR_X and PR_Y where country X is operating on social indifference curve I_1. Increases in PR_X (movements to the right) will only result in a constant welfare if it is matched by reductions in PR_Y. Small reductions in PR_X with PR_Y remaining unchanged, will normally increase welfare, and so for welfare to remain constant, PR_Y must increase. As reductions in PR_X get larger, however, welfare will remain constant only if there are reductions in both PR_X and PR_Y. Similarly, PRI_{X2} and PRI_{X3} are combinations of PR_X and PR_Y where the level of welfare is the same as along I_2 and I_3, respectively.[8] It

[7]Throughout it is assumed that there is free mobility of resources between fishing and manufacturing. As has been correctly pointed out in the past, this is not always the case. Rather there is a time lag of perhaps as much as a generation involved. This fact should be considered when making practical applications of the model.

[8]The curves will be concave from below. For reductions in allowable levels of effort, the greater the reduction, the greater is the increase in F_X that is necessary to keep welfare constant, and at the same time, the effect of decreases in the allowable

follows then that any distribution of property rights to the fishery represented by a point inside the area delineated by PRI_{X1} will lead to an improvement in welfare in country X over that which is obtained at the international open-access equilibrium. Note that because of the shape of the curve, welfare in country X can actually be increased in some cases where its allowable level of effort decreases while that for the other country goes up. This is possible because at the open-access equilibrium, country X can gain from switching some resources from producing effort to producing the other good and, up to a point, these gains are possible even if country Y increases effort. (Points A, B, C, D, F, and G are analogous to A′, B′, C′, D′, F′, and G′.) The reader should be aware by now of the similarity between these curves and trade indifference curves in international trade theory. Before using these curves in the analysis of the problem at hand, however, a few more points are in order. The short line through I_2 at F is meant to represent the slope of the PP curve if E_X remains constant and E_Y decreases so that country X is operating at F. A decrease in PR_Y will cause the slope of X's PP curve to decrease at every level of M_X.[9] As pictured here it has decreased from a positive to a negative. If it decreases such that it is steeper than the social indifference curve at that point, then the PRI curve will look like PRI_{X4}. That is, the PRI curve will not have a negatively sloped segment to the left of the open-access equilibrium amount of effort for country X. This means that reductions in the allowable level of effort in country X, with the amount in country Y held constant, will always result in a reduction in welfare for country X. Along the same line if country X pursues a local maximizing policy (i.e. it operates at point G in Figure 4a), the international equilibrium will be at point G′ in Figure 4b. This means that under no circumstances will country X be better off if it unilaterally decreases its allowable effort and it will always be worse off if country Y increases its level of effort. This is not the case if the international equilibrium is at point A′.

Figure 5a is similar to Figure 4b except that PRI curves for country Y have been added. PRI_{Y1} has the same meaning for country Y as does PRI_{X1} for country X and is constructed in an identical fashion.

Any distribution of property rights represented by a point inside the area delineated by PRI_{Y1} would result in an increase in the welfare of country Y. It follows then that any combination that is in the area common to both PRI_{X1} and PRI_{Y1} (see hatched area of Figure 5a) will increase the welfare of both countries over that achieved by the open-access "law of capture" distribution of the rights to the fishery. Note again that it is possible for both countries to be better off in some cases where the trade involves a reduction in property rights in one country and yet an increase in the other.

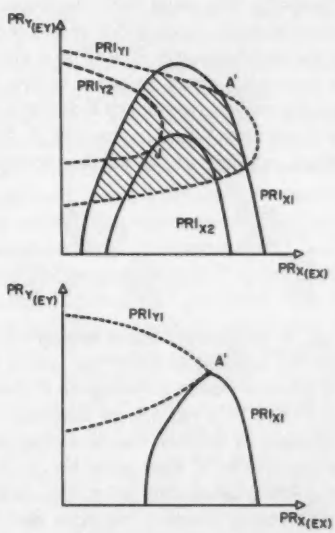

FIGURE 5.—The area common to the initial property right indifference (PRI) curves of both countries represents those distributions of the fishery where both countries will be better off than at the open-access equilibrium. In some special cases, there is no such area (see b).

level of effort in country Y on F_X decreases as E_X increases (i.e. $\frac{\partial F_X}{\partial E_Y} = -bE_X$). Therefore greater reductions in PR_Y will be necessary to compensate for equal reductions in PR_X as the amount of E_X is reduced from the international equilibrium level. For increases in PR_X, the greater the increase the smaller is the marginal increase in fish caught and yet the greater must be the increase in catch in order to keep welfare constant. Therefore greater reductions in PR_Y will be necessary to compensate for equal increases in PR_X as the amount of E_X is increased from the international equilibrium level.

[9] $$\frac{\partial F_X}{\partial M_X} = -(a - 2bE_X - bE_Y)\frac{G_2^X}{G_1^X}$$

and so

$$\frac{\partial\left(\frac{dF_X}{dM_X}\right)}{\partial E_Y} = b\,\frac{G_2^X}{G_1^X}.$$

Therefore, as E_Y decreases, the slope will decrease.

It is also possible that in some cases there may be no changes in both E_X and E_Y that will benefit both countries. If both countries adopt a local optimum regulation policy, the PRI's will be of the general shape of those depicted in Figure 5b. In this case, there have to be mutual reductions in order for either country to gain, but as pictured here, there are no mutual reductions that will benefit both countries.

If the governments have the power to control the level of effort in their countries, then it is possible for both of them to increase their welfare by each agreeing to a change in the property right distribution such that the new combination lies within the area described. And further gains are possible if the PRI's for the countries are not tangent at the new point. In other words, given that the equations for the PRI's are of the form $W_{PR} = W_{PR}(PR_X, PR_Y)$, further gains are possible unless

$$\frac{\frac{\partial W_{PR}^X}{\partial PR_X}}{\frac{\partial W_{PR}^X}{\partial PR_Y}} = \frac{\frac{\partial W_{PR}^Y}{\partial PR_X}}{\frac{\partial W_{PR}^Y}{\partial PR_Y}}, \qquad (15)$$

that is, unless the slopes of the PRI curves are equal. Formally this says that the ratio of the change in welfare in country X due to a change in property rights in country X and to a change in rights in country Y must be equal to the ratio of the change in welfare in country Y due to a change in rights in country X and in country Y. This can be rewritten in terms of the earlier notation as:

$$\frac{U_1^x \frac{\partial F_x}{\partial E_x} + U_2^x \frac{dM_x}{dE_x}}{U_1^x \frac{\partial F_x}{\partial E_y}} = \frac{U_1^y \frac{\partial F_y}{\partial E_x}}{U_1^y \frac{\partial F_y}{\partial E_y} + U_2^y \frac{dM_y}{dE_y}}. \qquad (15')$$

The change in welfare in either country due to a change in its allowable effort is equal to the change in welfare due to a change in F times the change in F due to a change in allowable effort plus the change in welfare due to a change in M times the amount of M that must be given up to produce the extra allowable effort. The change in welfare in the other country is simply the change in welfare due to a change in F times the change in F due to a change in allowable effort in the first country.

Where the final trading position will be and hence what the exact gain to each country is cannot be accurately determined in advance. It depends however upon the international free market equilibrium distribution of the property rights to the fishery which determine the position of the PRI's, the trading ability of the two countries, the extent of the knowledge concerning each other's PRI's, and the number and particular composition of any small trades that lead up the final equilibrium. It would be possible to construct offer curves from the PRI's similar to the ones used in international trade theory, but since trade in mutual changes in property rights will necessitate intergovernmental negotiations and since they will, more than likely, take place on a lump-sum basis, the equilibrium determined by their intersection would be of doubtful significance.

To summarize this discussion let us consider point J in Figure 5a, which is one possible final trading position. Notice that it is not possible to redistribute the property rights from that point without forcing one of the countries to suffer a loss in welfare; that is, there are no further changes in the distribution of the property rights that will be mutually beneficial. This is one of the conditions that must hold for an MEY of an international fishery. It determines the amount of fish that should be caught and the distribution of the rights to catch it. An important point to remember however is that this condition will not guarantee that the fish are caught at the lowest possible cost, and yet this is a very important aspect of MEY.

Let us now consider the potential for mutual gains from trade in actual property rights or in fishing effort. Such trade is not possible unless the rights to fish have been formalized either at the open-access equilibrium or at some other mutually agreed upon point. Again it should be remembered that this is only one type of trade, and the degree to which each country is willing to engage in it depends to some extent upon the makeup of the other trades.

Just because a country has the right to fish does not mean that it should necessarily produce the effort to catch the fish. For instance, if the opportunity cost of producing effort is cheaper in X, then both countries can gain if X expands the production of effort and then sells the increase to Y, who must make a corresponding reduction in its production of effort. If the price of effort for these international sales is between that in each country, both will be able to gain. Country X will gain because it is getting more for the effort that it cost to produce. Country Y will gain because it can buy

effort cheaper than it can produce it at home. These mutually beneficial trades can continue until the opportunity cost of producing effort is the same in both countries, i.e. until:

$$\frac{dM_X}{dE_X} = \frac{dM_Y}{dE_Y} . \tag{16}$$

The same thing could be accomplished by X purchasing rights to apply effort from Y until the MRT's for E and M are equal. Assume for simplicity that $P_F^Y = P_F^X$. Initially the price for a right to use one unit of effort would have to be somewhat above the rent the right-holder in Y would earn by doing the fishing himself. ($R_Y = P_F^Y \frac{F(\alpha)}{\alpha} - P_E^Y$, where α in this case is the total of the allowable efforts from both countries.) People in X will be able to pay more than that since P_E^X is less than P_E^Y.

In trade equilibrium the prices of fish and effort are the same in both countries, and therefore the rents in both countries will be identical and no further gains from trade are possible.

While the above will not change the amount of fish produced, it will make sure that effort is being produced at a minimum cost. The savings can be used to produce more of the manufactured good which can be distributed such that both countries are better off.

Now that two of the possible types of trade have been discussed, it will prove worthwhile to show exactly how they can be interrelated.

Trade in E or in fishing rights may have an effect on the bargaining for the distribution of property rights. To see this, assume that after such bargainings country X is at point D in Figure 4a and at that point $\frac{dM_X}{dE_X}$ is less than $\frac{dM_Y}{dE_Y}$. If it produces q more units of E but sells them to Y who reduces its production of E by the same amount, the PP curve will not change. Initially X will operate somewhere horizontally to the left of point D because it had to give up units of M_X to get the extra units of E. Y will be willing to pay sufficient units of M to X such that it will ultimately operate somewhere horizontally to the right of D and will therefore show an increase in welfare. Therefore at point D′ in Figure 4b, which represents the rights to fish and not the actual amount of E produced in each country, the welfare of X will increase. By similar analysis it can be shown that if trade is possible, Y will always be at a higher level of welfare at D′ also. This means that the PRI's of both X and Y will change shape and position. Therefore more than likely there will be the possibility of further mutually beneficial trades in the distribution of fishing rights.

The final type of trade to consider is trade in the final products M and F. If the relative prices are different in the two countries, mutually beneficial trades can be arranged. These trades can continue to be mutually beneficial until the marginal rate of substitution in both countries is the same, i.e. until:

$$\frac{U_2^X}{U_1^X} = \frac{U_2^Y}{U_1^Y} . \tag{17}$$

These trades will be affected by trades in E and also in changes in the allocation of the property rights.

On a practical note it must be admitted that few countries will be willing to let their international trade policy in all goods be dictated by their fishery management program. Therefore it is unrealistic to assume that they will drop all restrictions on international trade on this account.

This means that even after the rights to fish have been distributed, there are four things that can be traded: fish, manufactured goods, effort, and rights to fish. Because the prices of the last two are directly related to those of the first two, the relative demands for M and F will determine the equilibrium set of prices. It is impossible to predict, however, just what the actual trade bundle will be. For instance, nothing in the model allows us to predict whether X will export effort or import fishing rights if it has a comparative advantage in producing effort. The outcome of that, however, will affect its exports or imports of F.

Although the exact makeup of the international MEY position cannot be described, Conditions (15), (16), and (17) must hold simultaneously for it to be in effect. (Condition (15) sets a distribution from which no further mutual gains are possible, and Conditions (16) and (17) guarantee that Condition (14) above will hold for that distribution.) That is all potential mutual gains (where a mutual gain could consist of one country being made better off and the other remaining the same) by (1) altering the distribution of the rights to use effort, (2) trading in actual rights or in effort itself, or (3) trading in final goods, have been achieved. This point (say at point D in Figure 3) is a Pareto point that can be reached by mutually advanta-

geous trades between the two countries given their initial positions which include their productive capacity and the rights to the fishery that they have obtained by the right of capture. At this point there will be an MEY to the fishery. The proper amount of fish will be harvested and at the lowest cost possible. But since there is nothing sacred about these initial positions, point D is not inherently superior to any other point on the curve. If the world order somehow alters their initial positions, for instance, by saying that since Y is a poor country it should be able to expand its effort and X should do the opposite, the same types of trades will still be possible, and they will lead to a point on the curve that is more advantageous to country X than was point D. This point would also be an MEY given the distribution of productive capacity and of the wealth of the fishery. The distribution of the rights to the fishery is very important in determining the MEY of the fishery. Let us consider some of the practical implications of this discussion. First, before an international fishery can be optimally managed, the wealth from it must be distributed. The exact makeup of the distribution is not important, but it is possible, in most cases, to find a distribution whereby both countries are better off than at the initial bargaining point. The rights to the fishery should be transferable if the country owning them is to receive the maximum possible benefit. This way, it can sell the rights or hire effort from other countries to utilize them if it does not have a comparative advantage in producing effort. Therefore, unless the upcoming Law of the Sea Conference can agree to some sort of distribution of the wealth of the fishery and make allowances for possible trades in the makeup of the distribution bundle and also in fishing rights and effort, there is little hope for economically rational management of international fisheries.

The results of this two country, one fishery model can be expanded in a fairly straightforward fashion to a situation where there are many countries that simultaneously exploit several different fisheries. An international open-access equilibrium will occur when, in each country, the average returns from fishing the various stocks are equal to the average cost of providing effort. The distribution of the wealth from the fisheries will depend on the ability of each of the countries to produce the effort that is most efficient for a particular fishery. The more efficient producers will capture a larger share of the fisheries. If perfect international trade in fish products is not possible, then the distribution of the fishery by the "rule of capture" will also depend upon the tastes of the countries. A country that has the potential to harvest a certain type of fish very efficiently but has little desire for the product and cannot use it in international trade will not exploit that stock very extensively.

The usefulness of unilateral regulation in this situation will probably be less than in the two country case. Any reduction in effort will more than likely be met by an increase from one of the other countries. Therefore, while the country will show an increase in the amount of other products it can produce, it is entirely possible that the value of its total production will fall due to the decrease in catch.

Proper international regulation must take into account the effect that effort from one country will have on the yields to other countries exploiting the same stocks. With this consideration in mind, each country can benefit from some program of reallocation of the rights to the fish stocks from that which exists under open access. To achieve the maximum potential benefits, this program should include the possibility of trade in effort, fishing rights, and final products. The existence of many countries will of course make it much more difficult to specify the set of redistributions that would be beneficial to all concerned and even more difficult to get the countries to agree to one combination within that set. A major problem with international regulation is that allocational requirements are just as important as economic efficiency requirements. But given a mutually agreed upon allocation (i.e. a certain allowable level of effort in each country for all fisheries), the efficiency requirements can be met. The problem is to get agreement on a distribution plan with many different countries involved.

SUMMARY AND CONCLUSIONS

In the first section of the paper the general equilibrium model was used to derive the familiar result that in an open-access fishery too many resources will be allocated to the production of fishing effort. Using this model it is possible to explicitly take into account the lost production of other goods. In the second section the general equilibrium model was expanded to include two countries exploiting the same open-access fishery. The amount of effort used in one country will af-

fect the production possibilities in the other by changing the catch per unit of effort. Therefore, there is a direct technical relationship between the two countries. An international open-access equilibrium will exist when the average return to effort is equal to the marginal cost of providing it. (Whether or not such an equilibrium will ever be reached is another question.) The international optimum is where the marginal increase in the value of the fish caught (regardless of the country in which it is landed) is equal to the marginal cost of producing the last unit of effort in both countries. Using this model, two interesting points can be made. First, under open access, what are normally considered to be improvements in the terms of trade, for either the exporter or the importer of fish, can in some circumstances lead to a decrease in welfare. Also attempts at unilateral management can lead to decreases in welfare depending on the way in which the other country's fishing industry reacts. Proper regulation policies should directly take these things into account.

The topic of the third section was the necessary conditions for an MEY of an international fishery. The discussion with its implicit assumptions of governments that are willing and able to negotiate in an open and far ranging manner at zero cost, free trade in all goods, regulation methods that are not at the expense of efficiency, a physically independent fish stock that is only available to two countries, showed if negotiation is possible that an international MEY can be reached. This point will be the MEY of the fishery. (Even if the assumption about the possibility of free trade in final goods is dropped, the analysis of trade concerning the distribution of property rights to the fishery and trade in rights or effort is still valid. Therefore, even if there are different price and cost structures in the two countries, there is a basis for selecting a second best total amount and composition of fishing effort.)

It is also pointed out that there are many points that satisfy the conditions of an international MEY and that the distribution of the rights to the fishery (especially where the wealth from the fishery is large relative to the productive capacities of the countries) and, to a lesser extent, the differences in negotiating ability have an effect on which one will apply at any point in time. (There will not be one point that can be called MEY as in the case of a national fishery.) This is important because fishery negotiations typically work in the reverse. They try to find some optimum total amount of effort that should be applied and then they divide it in some equitable fashion, but it is impossible to choose an optimum amount unless the distribution has already been determined.

With regard to the argument that the underdeveloped countries should be granted preferential treatment in the distribution of the ocean's living resources, the model points out that if this is accepted, it does not mean that they should necessarily do the fishing. Rather, if they do not have a comparative advantage in the production of fishing effort, they would be better off by either selling their rights to the fish or by hiring fishing effort from other countries.

In conclusion this paper has formalized the analysis of the problems of international fisheries management that earlier writers only briefly discussed. To their list of problems of different prices, taste, and cost structures, it adds the effect that the distribution of the wealth of the fishery itself can have on the final outcome. It presents the three conditions for an MEY of an internationally utilized fishery. More generally the conditions guarantee the proper production bundle of all goods and its optimal distribution given the productive capacity of the countries and of the fishery and the distribution of wealth.

Although the discussion has been in terms of a fishery, the analysis could be expanded to other common property resources, such as air and watersheds, deep-sea mineral sources, etc. by taking proper consideration of the various physical characteristics of the resource involved.

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IMPACT OF THERMAL EFFLUENT FROM A STEAM-ELECTRIC STATION ON A MARSHLAND NURSERY AREA DURING THE HOT SEASON

WILLIAM E. S. CARR[1] AND JAMES T. GIESEL[2]

ABSTRACT

Seine samples of fishes were collected during the hot season from three similar marshland creeks situated at various distances from a steam-electric station near Jacksonville, Fla. Thermal effluent from the electric station is discharged directly into one creek and enters a second creek on the initial stage of each rising tide. The third creek remained at ambient temperature. Fishes collected in the samples were analyzed for species composition and for density and biomass per unit area. A total of 48 species belonging to 23 families were identified. Thirty-seven species were collected at least once in the ambient temperature creek whereas 30 species were collected in the creek receiving the maximum amount of thermal effluent.

Twenty species appearing in the samples are categorized as utilizable species because they are used by man either as food or for various fishery products. Specimens of all utilizable species were juveniles. In the thermally affected creeks, both the numbers and the biomass per unit area of juveniles of utilizable species were 3- to 10-fold smaller than those obtained in collections from the ambient temperature creek. When data for the entire hot season are considered, the creek receiving the largest input of thermal effluent supported a population of fishes having approximately 19% of its numbers and 32% of its biomass composed of juveniles of utilizable species. In contrast, the ambient temperature creek supported a population having approximately 73% of its numbers and 83% of its biomass composed of such species. Whereas juveniles of two species of mullet (*Mugil curema* and *M. cephalus*) accounted for the majority of the utilizable fishes using the thermally affected creeks as a nursery area, large numbers of juveniles of at least five additional utilizable species occupied the ambient temperature creek. These species were as follows (in order of decreasing abundance): tidewater silverside, *Menidia beryllina*; spot, *Leiostomus xanthurus*; Atlantic menhaden, *Brevoortia tyrannus*; silver perch, *Bairdiella chrysura*; and Atlantic thread herring, *Opisthonema oglinum*.

There is no longer any doubt that estuarine areas play a vital role in the life cycles of the majority of species of finfish and shellfish that are harvested annually in coastal fisheries. The role of estuaries as nursery areas for both sport and commercial species is now well documented (Skud and Wilson 1960; Smith et al. 1966; Sykes and Finucane 1966; Carr and Adams 1973; others). The majority of sport and commercial species must inhabit estuarine areas during at least part of their life cycles. Most frequently it is the early juvenile stages that exhibit the most pronounced estuarine dependence.

Thermal additions from power plants are considered to pose a potentially serious threat to valuable estuarine habitats. Krenkel and Parker (1969) have estimated that the amount of water required for condenser cooling by power plants in this country will increase from 50 trillion gallons per year in 1968 to 100 trillion gallons per year by 1980. This latter amount represents approximately one-fifth of the total land runoff in the contiguous United States. The immense volumes of water required for cooling by power plants are most readily obtained by building these plants adjacent to estuaries or in other coastal locations. The fact that estuarine areas "are among the most productive natural ecosystems in the world" (Schelske and Odum 1962) raises the question as to whether meeting the increasing needs for electricity by our growing population is best satisfied by using estuarine areas as the receiving waters for ever increasing discharges of thermal effluents.

Although a large literature exists concerning various biological facets of "thermal pollution" (reviews are provided by Naylor 1965; Wurtz and Renn 1965; Krenkel and Parker 1969; Jensen et al. 1969; Coutant 1970, 1971; Sylvester 1972; others) we are aware of no published studies that

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attempted to measure in situ the impact of thermal additions upon the capacity of an estuarine habitat to continue functioning as a viable nursery area, particularly for species of sport and commercial significance. Nugent (1970) provided one of the most complete studies on the effects of a thermal effluent on the estuarine macrofauna in the vicinity of a power station south of Miami, Fla. Nugent concluded that there were both beneficial and harmful effects attributable to the thermal additions but that the overall impact was "detrimental to many of the economically valuable animals of the waterway." Nugent found that during the hot summer months the heated effluent decreased the number of fishes present in the discharge area and also contributed to the death of certain organisms. However, the methods used in this study for the collection of fishes (gill nets, traps, and hoop nets) are unsuitable for the collection of many juvenile specimens and are somewhat inappropriate for estimates of density and standing crop. Grimes (1971) and Grimes and Mountain (1971) studied the effects of a thermal effluent upon marine fishes in the vicinity of a power station near Crystal River, Fla. Their major conclusions were that the natural seasonal abundance and the diversity of fishes were slightly altered by fishes being attracted into the heated area during late fall and early winter and by being repulsed during the summer. However the collecting methods and the station locations used in this study make the data difficult to assess in terms of the impact of the thermal effluent on the nursery area capacity of the affected area.

The current study was designed to evaluate in quantitative terms the impact that the discharge of a thermal effluent by a steam electric station had upon the capacity of an estuarine habitat to continue functioning as a nursery area during the hot season. This study was conducted in a marshland area to the northeast of Jacksonville, Fla. The data were obtained by analyzing the contents of seine samples taken from shallow-water stations located in three marshland creeks situated in the vicinity of the power station.

METHODS

Description of Study Area

San Carlos Creek, a small marshland creek draining into the St. Johns River, receives the discharge of thermal effluent from the Northside Generating Station (NGS) operated for the city of Jacksonville by the Jacksonville Electric Authority (see Figure 1). The NGS is situated in a relatively undeveloped marshland area to the northeast of Jacksonville approximately 10 miles west of the juncture of the St. Johns River with the Atlantic Ocean. Currently the NGS has two, of an anticipated three, oil-fired steam-electric units on line. Units 1 and 2 of the NGS (550-MW generating capacity) discharge approximately 280,000 gallons/min of thermal effluent directly into San Carlos Creek via outfalls situated 150 ft apart. The completion of Unit 3 (550 MW) in 1976 will result in the discharge of an additional 280,000 gallons/min of thermal effluent into this same creek. Cooling water for the NGS enters via a flume from the St. Johns River and the heated effluent is discharged into San Carlos Creek at a point approximately 0.75 mile upstream from the river.

San Carlos Creek and two other physically similar creeks located adjacent to the site described above were used for the collection of fishes described in the current study. San Carlos Creek not only receives directly the thermal effluent from

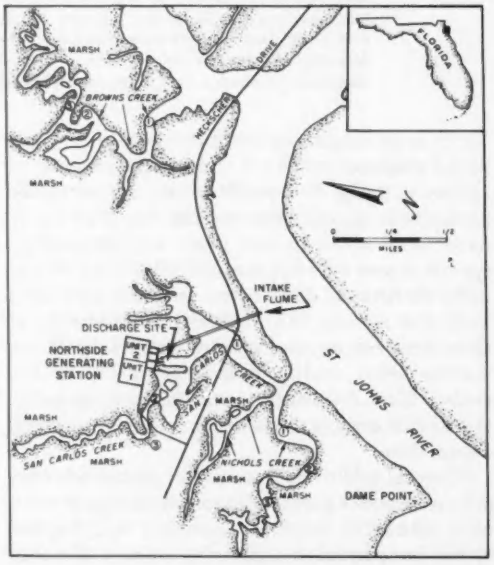

FIGURE 1.—Study area showing location of Northside Generating Station and marshland creeks adjacent to St. Johns River north of Jacksonville, Fla (see inset). Locations of sampling stations in San Carlos Creek, Nichols Creek, and Browns Creek are indicated by numbers. Juncture of river and ocean is situated about 10 miles to the east.

the NGS but on each rising tide this effluent is backed up by tidal action and much of it is retained within the confines of this creek. At this time the thermal effects extend to the uppermost reaches of the creek. A second creek, Nichols Creek (see Figure 1), receives an injection of thermal effluent during the initial stage of each rising tide. Nichols Creek converges with San Carlos Creek just prior to the juncture of both with the river. A major branch of a third creek, Browns Creek, is situated approximately 1 mile east of San Carlos Creek and is completely beyond the zone of thermal influence produced by the power plant. Browns Creek served as a "control" creek that remained at ambient temperature.

The three creeks are physically quite similar in terms of their size, depth, and contiguous marshland and upland areas. The substrate in each consists primarily of soft black mud rich in organic material. Scattered bars of a firmer sand-mud composition are present. Each creek is lined on either side with marsh grasses, primarily *Spartina alterniflora* and *Juncus roemarianus*. No submerged sea grass or other attached macrophytes are present in the creek beds themselves. The major variables affecting differentially the habitats of the three creeks are the thermal effluent, the chemical agents used in the cleaning of condenser tubes, and the clearing and alteration of the landscape necessary for the construction of the power plant.

Sampling Stations

Three sampling stations were established in each of the three creeks (see Figure 1). One of the stations in each creek was situated near the creek mouth whereas the other two were situated at appropriate distances upstream. The station sites in each creek were selected such that two stations were situated at the sites of juncture of small adjoining creeklets and the third at the edge of a bar. During the hot season of 1973, samples were taken from all nine stations during June and July and from seven of the stations in September.

Collecting Methods

Fishes were collected at all stations with a bag seine (50 × 6 ft) constructed of 3/8-inch stretch mesh netting. The dimensions of the area seined in each sample were measured with a steel tape at the time the sample was taken. Areas sampled at the stations varied somewhat according to the particular configuration of each seine haul; these areas ranged from 102 to 403 m^2 per station. During each sampling period, all seine hauls were made during the day on consecutive days within 1.5 h of low tide. Specimens were preserved immediately in 20% Formalin[3]-seawater and later washed with tap water and stored in 75% isopropyl alcohol. Determinations of biomass are based on weights of preserved specimens. Invertebrates obtained in the samples were also retained for future analysis.

A Beckman electrodeless induction salinometer was used to obtain measurements of temperature and salinity.

Quantitative core samples and plankton samples were also taken but their analyses are incomplete and they are not reported here.

Presentation of Data

To minimize the number of tables and figures necessary for the presentation of data, analyses of the samples taken from the three stations in each creek have been pooled for each monthly collection. Although this method prohibits comparisons of variations between individual stations within a particular creek, this procedure provides a more direct means of analyzing and comparing the overall population structure within each creek.

RESULTS

Table 1 presents temperature and salinity measurements taken from San Carlos Creek, Nichols Creek, and Browns Creek during the study period. The temperature data from Browns Creek, which is beyond the range of thermal influence produced by the power station, can be used as a measure of the daytime ambient temperature regime for a creek in this area. During the June sampling period, the average recorded temperature of water discharged by Units 1 and 2 of the NGS into San Carlos Creek was from 5.6° to 7.7°C above the average temperatures recorded at the three stations in Browns Creek. During July, San Carlos Creek received water from the power station that averaged 8.0° to 8.9°C higher than the averages recorded in Browns Creek. During September, this differential increased to 9.1° to 10.8°C. The highest temperature that we recorded

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Daytime measurements of temperature and salinity recorded during the hot season of 1973 from three creeks in the vicinity of the Northside Generating Station, Jacksonville, Fla.

Item	San Carlos Creek			Nichols Creek			Brown Creek			Outfalls in San Carlos Creek	
	Stn. 1	Stn. 2	Stn. 3	Stn. 1	Stn. 2	Stn. 3	Stn. 1	Stn. 2	Stn. 3	Unit 1	Unit 2
23-27 June:											
Temperature, °C:											
Maximum	35.9	35.0	36.4	31.1	32.6	34.6	30.5	30.5	[1]27.9	36.5	37.8
Minimum	30.3	31.0	30.0	27.8	28.2	27.6	26.7	26.9		31.8	33.9
Average	33.1	33.1	33.5	29.4	29.9	30.2	28.5	28.5		34.1	36.2
Salinity, ‰:											
Maximum	30.6	30.1	29.0	27.0	26.6	25.6	27.5	26.2	[1]21.7	31.0	31.0
Minimum	20.7	24.7	18.2	18.9	18.3	18.7	18.3	17.7		23.3	24.2
Average	25.9	27.3	25.6	21.9	21.9	21.7	22.6	22.3		26.5	26.8
25-26 July:											
Temperature, °C:											
Maximum	38.0	38.2	39.2	37.5	37.3	35.8	31.2	30.6	31.6	39.7	39.4
Minimum	30.4	33.9	32.8	30.1	30.4	31.6	29.2	29.7	29.8	36.9	38.5
Average	35.3	35.7	35.5	32.3	32.4	32.9	30.2	30.2	30.5	38.5	39.1
Salinity, ‰:											
Maximum	31.2	29.8	31.0	31.5	31.3	29.3	27.5	27.3	27.2	30.8	30.8
Minimum	23.3	26.2	26.6	23.5	23.6	24.1	25.5	21.8	21.7	25.7	25.2
Average	28.1	28.9	28.8	27.4	27.6	26.0	26.5	25.2	25.1	29.2	29.2
19-20 September:											
Temperature, °C:											
Maximum	37.3	37.7	37.9	36.2	—[2]	35.0	29.7	29.6	27.5	37.6	38.4
Minimum	30.6	32.3	32.1	28.5		27.9	27.3	26.5	27.0	37.4	37.8
Average	34.3	36.2	36.3	31.5		31.4	28.4	27.9	27.3	37.5	38.1
Salinity, ‰:											
Maximum	26.4	24.3	24.3	24.8	—[2]	24.7	27.2	26.2	26.4	23.2	24.0
Minimum	19.5	22.1	22.7	18.1		21.6	21.9	20.8	19.6	20.6	21.0
Average	22.0	23.2	23.5	22.4		23.4	24.6	22.7	23.0	22.0	22.5

[1]Only one recording.
[2]Not recorded.

was 39.7°C taken at the outfall of Unit 2. The data shown in Table 1 suggest that the thermal regime present in Nichols Creek was somewhat intermediate between that of the other two creeks. However this is not entirely the case. During the initial phase of each rising tide, tidal action causes the injection of heated effluent from the power plant up the entire length of Nichols Creek. On 19 September, we recorded this injection as it reached and later passed Station 1 in this creek (see Figure 2). The highest temperature recorded at Station 1 during this day was 36.2°C. The passage time of this injection of hot water was approximately 2 h with temperatures greater than 34°C lasting approximately 1 h. Only a slight drop in temperature was apparent when the hot water reached Station 3 situated approximately 0.6 mile away (see Figure 2). Hence, whereas the minimum and average temperatures in Nichols Creek are more similar to those of Browns Creek than to those in San Carlos Creek, the maximum temperatures in Nichols Creek are more similar to those in San Carlos Creek. Consequently, at the onset of each rising tide (twice daily), organisms living in Nichols Creek are subjected to a period of 1- or 2-h duration during which the water temperature is markedly above ambient and almost as high as that in San Carlos Creek.

Table 2 provides a list of the species of fishes collected from the three creeks during the hot season of 1973. A total of 48 species belonging to 23 families were collected. Aside from the Cyprinodontidae and certain of the Gerreidae and

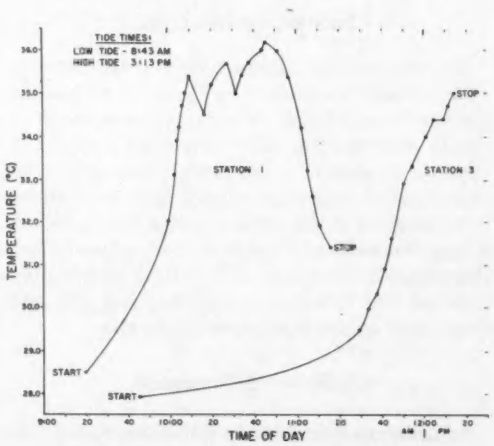

FIGURE 2.—Recordings of water temperature taken in Nichols Creek on the initial stage of rising tide, 19 September 1973. Appearance of thermal effluent from the power plant is indicated by the sudden increases in temperature at Stations 1 and 3.

TABLE 2.—List of fishes collected during the hot season of 1973 from three creeks in the vicinity of the Northside Generating Station, Jacksonville, Fla.

Family	Scientific name	Common name[1]	Class[2]	Species utilized[3]
Elopidae	*Elops saurus*	Ladyfish	J	X
Clupeidae	*Brevoortia tyrannus*[4]	Atlantic menhaden	J	X
	Opisthonema oglinum	Atlantic thread herring	J	X
Engraulidae	*Anchoa hepsetus*	Striped anchovy	J	
	Anchoa mitchilli	Bay anchovy	J	
Synodontidae	*Synodus foetens*	Inshore lizardfish	J	
Ariidae	*Arius felis*	Sea catfish	J	
Batrachoididae	*Opsanus tau*	Oyster toadfish	J	
Belonidae	*Strongylura marina*	Atlantic needlefish	J	
Cyprinodontidae	*Cyprinodon variegatus*	Sheepshead minnow	J-A	
	Fundulus grandis	Gulf killifish	J-A	
	Fundulus heteroclitus	Mummichog	J-A	
	Fundulus majalis[5]	Striped killifish	J-A	
Poeciliidae	*Gambusia affinis*	Mosquitofish	J-A	
	Poecilia latipinna	Sailfin molly	J-A	
Atherinidae	*Menidia beryllina*	Tidewater silverside	J	X
Syngnathidae	*Syngnathus floridae*	Dusky pipefish	J	
Carangidae	*Caranx hippos*	Crevalle jack	J	X
	Chloroscombrus chrysurus	Atlantic bumper	J	
	Selene vomer	Lookdown	J	
	Trachinotus falcatus	Permit	J	X
Lutjanidae	*Lutjanus griseus*	Gray snapper	J	X
Gerreidae	*Diapterus olisthostomus*	Irish pompano	J	
	Eucinostomus argenteus	Spotfin mojarra	J-A	
	Eucinostomus gula	Silver jenny	J	
	Gerres cinereus	Yellowfin mojarra	J	X
Sparidae	*Archosargus probatocephalus*	Sheepshead	J	X
	Lagodon rhomboides	Pinfish	J	X
Sciaenidae	*Bairdiella chrysura*	Silver perch	J	X
	Cynoscion nebulosus	Spotted seatrout	J	X
	Leiostomus xanthurus	Spot	J	X
	Micropogon undulatus	Atlantic croaker	J	X
	Pogonias cromis	Black drum	J	X
	Sciaenops ocellata	Red drum	J	X
Ephippidae	*Chaetodipterus faber*	Atlantic spadefish	J	X
Mugilidae	*Mugil cephalus*	Striped mullet	J	X
	Mugil curema	White mullet	J	X
Gobiidae	*Gobionellus boleosoma*	Darter goby	J	
	Gobionellus hastatus	Sharptail goby	J-A	
	Gobionellus smaragdus	Emerald goby	J	
	Gobiosoma bosci	Naked goby	J	
	Microgobius gulosus	Clown goby	J-A	
Triglidae	*Prionotus tribulus*	Bighead searobin	J	
Bothidae	*Citharichthys spilopterus*	Bay whiff	J	
	Etropus crossotus	Fringed flounder	J	
	Paralichthys lethostigma	Southern flounder	J	X
Cynoglossidae	*Symphurus plagiusa*	Blackcheek tonguefish	J	
Tetraodontidae	*Sphoeroides nephelus*	Southern puffer	J	

[1]Common names recommended by Bailey (1970) are used.
[2]J = juvenile; A = adult.
[3]Species utilized refers to either sport species or to species cited by Lyles (1969:463-487) as being used by man for food or related fishery products.
[4]Some of these specimens may have been *B. smithii* and/or hybrids of *Brevoortia smithii* as described by Dahlberg (1970). Since they were all juvenile specimens the major characters given by Dahlberg for distinguishing between the three possibilities were extremely difficult to apply with certainty.
[5]According to Carter R. Gilbert (pers. commun.) of the Florida State Museum, some of these specimens may have been *F. similis*. The taxonomic status of the two species on the northeast coast of Florida is somewhat uncertain.

Gobiidae, all of the specimens were juveniles that were using the creeks as a nursery area. Twenty of the species are utilized directly by man, i.e., are species used for food and/or related fishery products including sport species and bait fishes. Subsequent references to "utilizable species" refer to those used by man as defined above.

Tables 3-5 provide monthly summaries of the numbers of individuals and the estimated densities of all fish species collected from the three creeks. Of the 48 species obtained in one or more collections, 30 were collected at least once in San Carlos Creek, 23 were collected in Nichols Creek, and 37 appeared in Browns Creek. Four species, *Cyprinodon variegatus* and three species of gobies (*Gobionellus smaragdus*, *Gobiosomo bosci*, and *Microgobius gulosus*), were collected only in San Carlos Creek thereby suggesting that they preferred the high temperature regime afforded there. However, the three species of gobies appeared only in the June samples. Eleven other species of temperature tolerant fishes were present in San Carlos Creek at densities that were either as great, or greater, than the densities present in the ambient temperature creek. These species were as follows (in order of decreasing

TABLE 3.—Collections of fishes from three stations on San Carlos Creek during the hot season of 1973. Area seined in June was 706 m², in July was 563 m², and in September was 563². Total area seined was 1,832 m².

Family	Species	June collection		July collection		September collection		Total collections	
		No.	No./100 m²	No.	No./100 m²	No.	No./100 m²	No.	No./100 m²
Elopidae	*Elops saurus*	3	0.4	—	—	1	0.2	4	0.2
Clupeidae	*Brevoortia tyrannus*	—	—	4	0.7	—	—	4	0.2
	Opisthonema oglinum	—	—	6	1.1	—	—	6	0.3
Engraulidae	*Anchoa hepsetus*	1	0.1	—	—	—	—	1	0.05
Belonidae	*Strongylura marina*	1	0.1	—	—	—	—	1	0.05
Cyprinodontidae	*Cyprinodon variegatus*	10	1.4	4	0.7	12	2.1	26	1.4
	Fundulus grandis	62	8.8	161	28.6	179	31.6	402	21.9
	Fundulus heteroclitus	192	27.2	669	118.8	405	72.1	1266	69.2
	Fundulus majalis	15	2.1	44	7.8	50	8.9	109	5.9
Poeciliidae	*Gambusia affinis*	—	—	5	0.9	2	0.4	7	0.4
	Poecilia latipinna	40	5.7	44	7.8	31	5.5	115	6.3
Atherinidae	*Menidia beryllina*	2	0.3	—	—	5	0.7	7	0.4
Lutjanidae	*Lutjanus griseus*	—	—	—	—	4	0.7	4	0.2
Gerreidae	*Diapterus olisthostomus*	—	—	—	—	1	0.2	1	0.05
	Eucinostomous argenteus	137	19.4	36	6.4	693	123.1	866	47.3
	Eucinostomous gula	—	—	—	—	3	0.5	3	0.2
	Gerres cinereus	1	0.1	2	0.4	3	0.5	6	0.3
Sparidae	*Lagodon rhomboides*	1	0.1	—	—	—	—	1	0.05
Sciaenidae	*Cynoscion nebulosus*	1	0.1	—	—	2	0.4	3	0.2
	Leiostomus xanthurus	44	6.2	—	—	—	—	44	2.4
	Pogonias cromis	4	0.6	—	—	—	—	4	0.2
	Sciaenops ocellata	1	0.1	—	—	—	—	1	0.05
Mugilidae	*Mugil cephalus*	40	5.7	13	2.3	1	0.2	54	2.9
	Mugil curema	211	29.9	292	51.9	42	7.5	545	29.7
Gobiidae	*Gobionellus boleosoma*	5	0.7	—	—	—	—	5	0.3
	Gobionellus hastatus	12	1.7	2	0.4	—	—	14	0.8
	Gobionellus smaragdus	2	0.3	—	—	—	—	2	0.1
	Gobiosoma bosci	1	0.1	—	—	—	—	1	0.05
	Microgobius gulosus	3	0.4	—	—	—	—	3	0.2
Bothidae	*Citharichthys spilopterus*	3	0.4	—	—	—	—	3	0.2
	Total	792	111.9	1,282	227.8	1,434	254.6	3,508	191.5
	Total utilizable species	308	43.5	317	56.4	58	10.2	683	37.1

abundance): *Fundulus heteroclitus*, *Eucinostomous argenteus*, *Mugil curema*, *F. grandis*, *Poecilia latipinna*, *F. majalis*, *Gobionellus hastatus*, *Gambusia affinis*, *Gerres cinereus*, *Elops saurus*, and *Lutjanus griseus*.

Eleven species, *Synodus foetens*, *Opsanus tau*, *Syngnathus floridae*, *Chloroscombrus chrysurus*, *Selene vomer*, *Micropogon undulatus*, *Chaetodipterus faber*, *Prionotus tribulus*, *Etropus crossotus*, *Paralichthys lethostigma*, and

TABLE 4.—Collections of fishes from three stations on Nichols Creek during the hot season of 1973. Area seined in June was 819 m², in July was 815 m², and in September 714 m². Total area seined was 2,348 m².

Family	Species	June collection		July collection		September collection[1]		Total collections	
		No.	No./100 m²	No.	No./100 m²	No.	No./100 m²	No.	No./100 m²
Clupeidae	*Brevoortia tyrannus*	1	0.1	—	—	—	—	1	0.04
Engraulidae	*Anchoa mitchilli*	36	4.4	—	—	—	—	36	1.5
Ariidae	*Arius felis*	—	—	1	0.1	—	—	1	0.04
Cyprinodontidae	*Fundulus grandis*	77	9.4	55	6.7	—	—	132	5.6
	Fundulus heteroclitus	346	42.2	766	94.0	10	1.4	1122	47.8
	Fundulus majalis	4	0.5	4	0.5	—	—	8	0.3
Poeciliidae	*Poecilia latipinna*	—	—	12	1.5	—	—	12	0.5
Atherinidae	*Menidia beryllina*	13	1.6	11	1.3	102	14.3	126	5.4
Carangidae	*Caranx hippos*	—	—	—	—	2	0.3	2	0.1
	Trachinotus falcatus	—	—	1	0.1	—	—	1	0.04
Gerreidae	*Diapterus olisthostomus*	1	0.1	—	—	—	—	1	0.04
	Eucinostomous argenteus	168	20.5	246	30.2	103	14.4	517	22.0
	Eucinostomous gula	—	—	49	6.0	12	1.7	61	2.6
Sparidae	*Archosargus probatocephalus*	—	—	1	0.1	—	—	1	0.04
	Lagodon rhomboides	—	—	1	0.1	—	—	1	0.04
Sciaenidae	*Bairdiella chrysura*	—	—	—	—	1	0.1	1	0.04
	Leiostomus xanthurus	105	12.8	47	5.8	6	0.8	158	6.7
	Pogonias cromis	—	—	1	0.1	—	—	1	0.04
Mugilidae	*Mugil cephalus*	121	14.8	7	0.9	1	0.1	129	5.5
	Mugil curema	653	79.7	183	22.5	35	4.9	871	37.1
Gobiidae	*Gobionellus boleosoma*	1	0.1	—	—	—	—	1	0.04
	Gobionellus hastatus	1	0.1	—	—	—	—	1	0.04
Bothidae	*Citharichthys spilopterus*	8	1.0	—	—	1	0.1	9	0.4
Cynoglossidae	*Symphurus plagiusa*	2	0.2	—	—	—	—	2	0.1
	Total	1,537	187.5	1,385	169.9	273	38.1	3,195	136.0
	Total utilizable species	893	109.0	252	30.9	147	20.5	1,292	55.0

[1]Station 2 not sampled in September due to mechanical problems.

TABLE 5.—Collections of fishes from three stations on Browns Creek during the hot season of 1973. Area seined in June was 685 m², in July was 676 m², and in September was 285 m². Total area seined was 1,646 m².

Family	Species	June collection		July collection		September collection[1]		Total collections	
		No.	No./100 m²	No.	No./100 m²	No.	No./100 m²	No.	No./100 m²
Elopidae	*Elops saurus*	—	—	1	0.1	—	—	1	0.06
Clupeidae	*Brevoortia tyrannus*	551	80.4	420	62.1	—	—	971	59.0
	Opisthonema oglinum	—	—	103	15.2	—	—	103	6.3
Engraulidae	*Anchoa hepsetus*	21	3.1	—	—	1	0.4	22	1.3
	Anchoa mitchilli	265	38.7	377	55.8	16	5.6	658	40.0
Synodontidae	*Synodus foetens*	3	0.4	—	—	1	0.4	4	0.2
Batrachoididae	*Opsanus tau*	1	0.1	—	—	1	0.4	2	0.1
Belonidae	*Strongylura marina*	1	0.1	—	—	—	—	1	0.06
Cyprinodontidae	*Fundulus grandis*	2	0.3	3	0.4	1	0.4	6	0.4
	Fundulus heteroclitus	717	105.0	342	50.6	9	3.5	1,068	64.9
	Fundulus majalis	1	0.1	—	—	—	—	1	0.06
Poeciliidae	*Gambusia affinis*	2	0.3	4	0.6	6	2.1	12	0.7
Atherinidae	*Menidia beryllina*	222	32.4	2,288	338.5	80	28.1	2,590	157.4
Syngnathidae	*Syngnathus floridae*	1	0.1	—	—	1	0.4	2	0.1
Carangidae	*Caranx hippos*	1	0.1	1	0.1	1	0.4	3	0.2
	Chloroscombrus chrysurus	—	—	—	—	2	0.7	2	0.1
	Selene vomer	2	0.3	1	0.1	—	—	3	0.2
Lutjanidae	*Lutjanus griseus*	—	—	1	0.1	4	1.4	5	0.3
Gerreidae	*Eucinostomus argenteus*	14	2.0	79	11.7	44	15.4	137	8.3
	Eucinostomus gula	2	0.3	44	6.5	2	0.7	48	2.9
	Gerres cinereus	—	—	1	0.1	—	—	1	0.06
Sparidae	*Lagodon rhomboides*	10	1.5	1	0.1	—	—	11	0.7
Sciaenidae	*Bairdiella chrysura*	77	11.2	38	5.6	4	1.4	119	7.2
	Cynoscion nebulosus	—	—	—	—	1	0.4	1	0.06
	Leiostomus xanthurus	912	133.0	134	19.8	25	8.8	1,071	65.1
	Micropogon undulatus	9	1.3	2	0.3	—	—	11	0.7
	Sciaenops ocellata	4	0.6	—	—	—	—	4	0.2
Ephippidae	*Chaetodipterus faber*	—	—	2	0.3	—	—	2	0.1
Mugilidae	*Mugil cephalus*	61	8.9	31	4.6	1	0.4	93	5.7
	Mugil curema	238	34.7	206	30.5	21	7.4	465	28.3
Gobiidae	*Gobionellus boleosoma*	1	0.1	1	0.1	—	—	2	0.1
Triglidae	*Prionotus tribulus*	—	—	1	0.1	—	—	1	0.06
Bothidae	*Citharichthys spilopterus*	5	0.7	4	0.6	—	—	9	0.6
	Etropus crossotus	—	—	—	—	1	0.4	1	0.06
	Paralichthys lethostigma	1	0.1	—	—	—	—	1	0.06
Cynoglossidae	*Symphurus plagiusa*	1	0.1	13	1.9	—	—	14	0.9
Tetraodontidae	*Sphoeroides nephelus*	2	0.3	—	—	2	0.7	4	0.2
	Total	3,127	456.2	4,098	605.8	224	79.4	7,449	452.7
	Total utilizable species	2,086	304.2	3,229	477.0	137	48.3	5,452	331.4

[1]Station 1 not sampled in September due to mechanical problems.

Sphoeroides nephelus, were collected only in Browns Creek and not in either of the thermally affected creeks. However, none of the species listed above made a major contribution to the total density of fishes in this ambient temperature creek. Among the other species entirely absent from San Carlos collections, only two species, *Anchoa mitchilli* and *Bairdiella chrysura*, made a significant contribution to the fish density in Browns Creek. When considered alone, the differences cited above might be construed to suggest that the nursery capacity of thermally affected San Carlos Creek is not markedly different from that of Browns Creek which functions at ambient temperature. However, a critical comparison of the densities, the biomasses, and the population structure of the fishes in the three creeks reveal some important differences that are described below.

Figure 3 illustrates the relative densities of both total fishes and utilizable fishes as they appeared in the monthly samples. The figure shows that the following three major differences existed between the populations present in the thermally affected creeks (San Carlos and Nichols) and the population present in the ambient temperature creek (Browns):

1. In June and July the density of total fishes was highest in the ambient temperature creek.
2. Throughout the entire study period the density of utilizable species was markedly higher in the ambient temperature creek.
3. In the ambient temperature creek, the majority of the population consisted of juveniles of utilizable species, whereas in the thermally affected creeks the majority consisted of species not utilized by man.

In June and July the estimated density of total

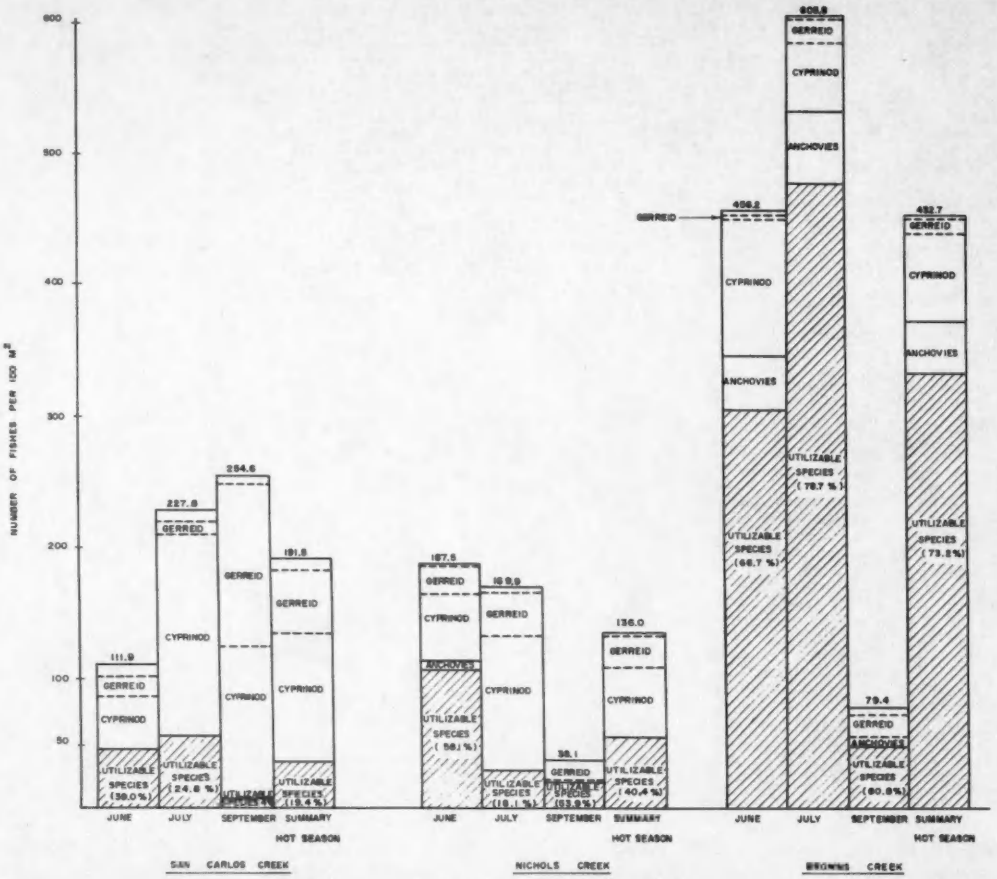

FIGURE 3.—Densities of fishes in the three creeks as estimated from seine collections. Species used by man as food or fishery products are combined and termed Utilizable Species. Percent of each collection that was represented by utilizable species is indicated. Cyprinod = all species of Cyprinodontidae. Gerreid = all species of Gerreidae except for *Gerres cinereus*. The histogram for each creek depicting "Summary Hot Season" was compiled on the basis of the total area sampled during the entire study period.

fishes in Browns Creek was three to four times higher than the estimated density in San Carlos Creek. However, in September the estimated density in San Carlos Creek was about three times higher than that in Browns Creek. The basis for this apparent September reversal between the two creeks was due primarily to the expected early fall emigration of juveniles of migratory species, many of which are utilizable species. The estimated density of total fishes in Browns Creek was two to four times higher than the density in Nichols Creek throughout the entire study period.

Of greater significance than the differences in total density of fishes described above, are the marked differences that existed between creeks in the estimated densities of utilizable species (see Figure 3). In June and July, the estimated density of utilizable species in Browns Creek was seven to eight times greater than in San Carlos Creek. In September following the emigration of juveniles of many migratory species, the estimated density of utilizable species in Browns Creek was still nearly five times greater than that recorded in San Carlos Creek. When data for the entire hot season are pooled, Browns Creek displayed an overall density of utilizable species approximately nine times greater than that in San Carlos Creek. In Nichols Creek the estimated densities of utilizable species were generally somewhat higher than those in San Carlos Creek yet markedly lower than those

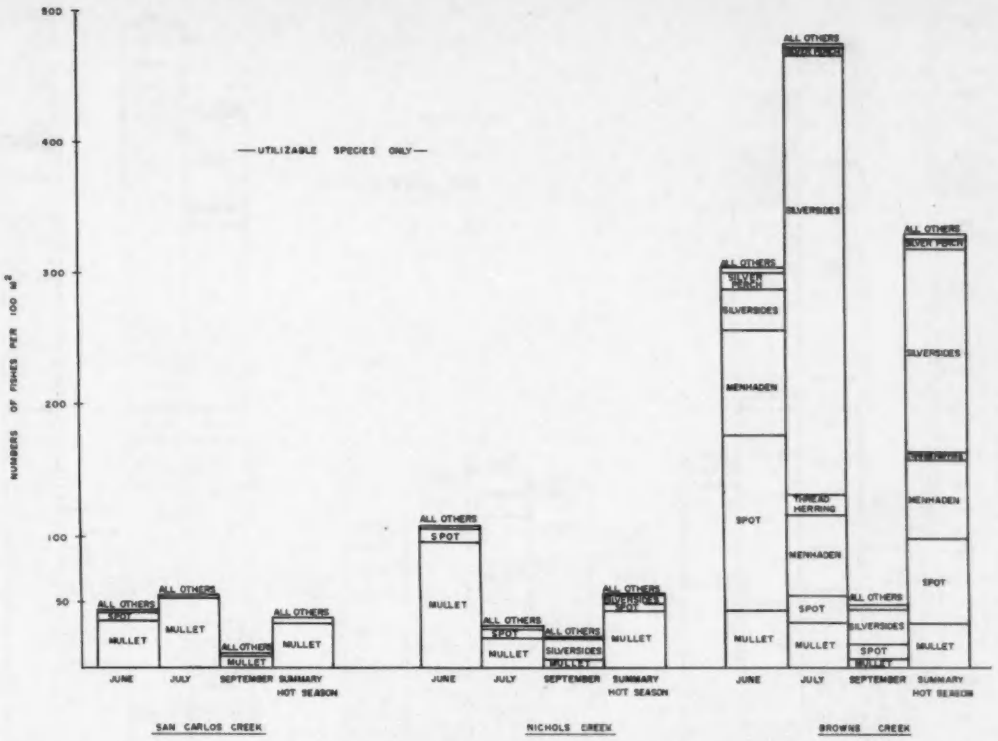

FIGURE 4.—Densities of utilizable species in the three creeks as estimated from seine collections. Histograms depicting "Summary Hot Season" compiled as described in Figure 3.

in Browns Creek. The injection of hot water that was forced through Nichols Creek twice each day (see Figure 2) obviously decreased the value of this second creek as a nursery area for utilizable species.

Figure 3 also illustrates the change in overall population structure that has occurred in response to the thermal effluent. Whereas in Browns Creek 61 to 79% (average 73.2%) of the total fishes in the monthly collections were utilizable species, in San Carlos Creek only 4 to 39% (average 19.4%) of the total specimens could be so categorized. Hence in contrast to the situation in the ambient temperature creek, the majority of the fishes occupying San Carlos Creek during the hot season are species not utilized by man. Dominant among this latter group of temperature tolerant fishes were two species of cyprinodonts (*Fundulus grandis* and *F. heteroclitus*) and the gerreid *Eucinostomous argenteus*. Whereas these three species alone accounted for 72% of the total fishes collected in San Carlos Creek, these same species accounted for only 16% of the total fishes collected in Browns Creek. In Nichols Creek the portion of the population consisting of utilizable species was generally greater than that in San Carlos Creek yet considerably less than that in Browns Creek.

Figure 4 illustrates the relative abundance of the various utilizable species collected in the three creeks. In San Carlos Creek, two species of mullet (*Mugil curema* and *M. cephalus*) alone accounted for 76 to 96% of the total utilizable species collected. In Browns Creek, mullet accounted for only 8 to 16% of the utilizable species. Five other species made major contributions to the array of utilizable species present in Browns Creek. These other species were (in order of decreasing abundance): tidewater silverside *Menidia beryllina*, spot *Leiostomus xanthurus*, Atlantic menhaden *Brevoortia tyrannus*, silver perch *Bairdiella chrysura*, and Atlantic thread herring *Opisthonema oglinum*. Silver perch *Bairdiella chrysura* were entirely absent from the San Carlos collections.

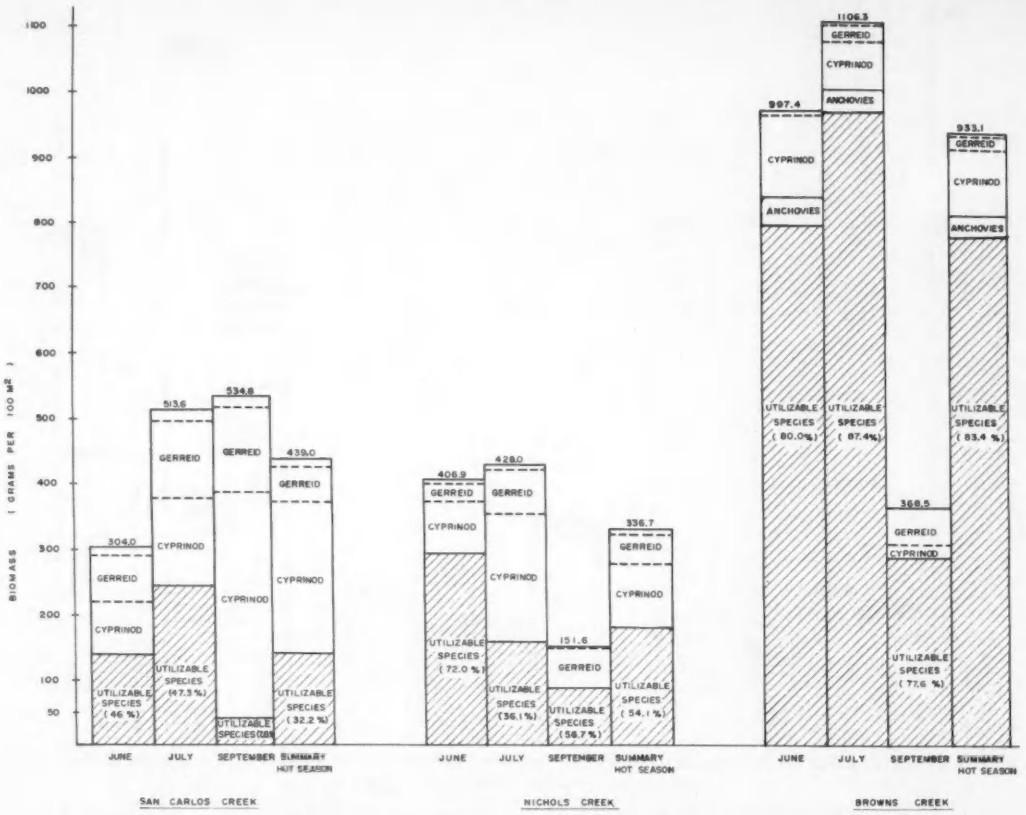

FIGURE 5.—Biomass per 100 m² of fishes in the three creeks as estimated from seine collections. Presentation as in Figure 3.

Figure 5 illustrates the biomass distributions that were computed from the weights of fishes obtained in the samples. The figure shows that the differences in overall standing crops (grams per 100 m²) between the creeks conform quite closely to the differences in density described earlier. In June and July the estimated standing crop of total fishes in Browns Creek was approximately 2 to 3 times greater than that in San Carlos Creek and 2.5 times greater than that in Nichols Creek. In September, following the aforementioned emigration of juveniles of many transient species, the estimated standing crop in San Carlos Creek was 1.5 times greater than that in Browns Creek. However, even in September, Browns Creek continued to support a standing crop approximately 2.5 times greater than that in Nichols Creek.

Of greater significance than the overall differences in biomass described above, are the marked differences in utilizable species that existed between creeks. Throughout the entire collecting period, the biomass of utilizable species (grams per 100 m²) was from four to seven times greater in Browns Creek than in San Carlos Creek and from three to six times greater in Browns Creek than in Nichols Creek. Whereas in Browns Creek the bulk of the biomass was distributed among utilizable species, in San Carlos Creek the bulk of the biomass was distributed among species not utilized by man. In San Carlos Creek, three species of nonutilized fishes (*F. grandis*, *F. heteroclitus*, and *E. argenteus*) accounted collectively for 45 to 85% (average 62%) of the total biomass. In Browns Creek these same species accounted for only 8 to 16% (average 11.9%) of the total biomass.

Figure 6 illustrates the biomass distributions among the various utilizable species. In San Carlos Creek, the two species of mullet alone accounted for 73 to 97% (average 86.7%) of the

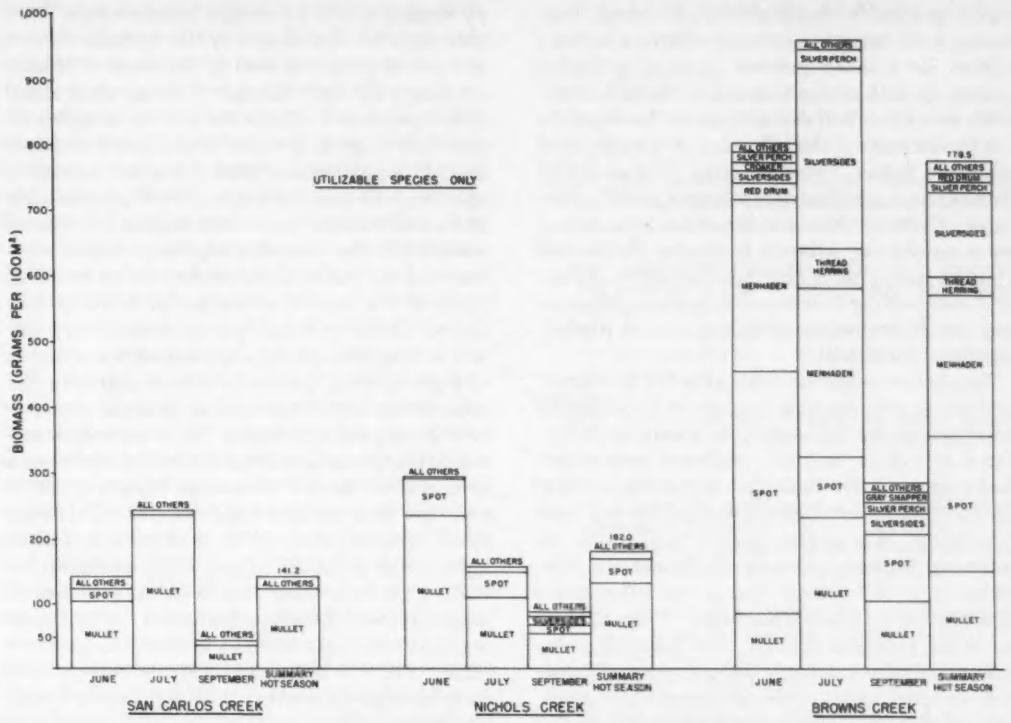

FIGURE 6.—Biomass per 100 m² of utilizable species in the three creeks as estimated from seine collections. Histograms depicting "Summary Hot Season" compiled as described in Figure 3.

biomass of utilizable species. In Browns Creek, the mullet accounted for only 11 to 37% (average 19.2%) of this biomass. The same five species that were cited earlier made the most significant additional contributions to the biomass of utilizable species in Browns Creek.

DISCUSSION AND SUMMARY

Elevated water temperature resulting from the discharge of condenser cooling water by the two units of the Northside Generating Station in Jacksonville, Fla. has a detrimental effect on the capacity of two marshland creeks to serve as a nursery area for juvenile fishes during the hot season. Evidence for this detrimental effect is based upon the marked differences in both the density of fishes and the species composition which exist between an ambient temperature creek and two creeks receiving thermal effluent. To the best of our knowledge this is the first field study in which quantitative measurements have been reported on the effects of a thermal effluent on the capacity of an estuarine receiving water to continue serving as a nursery area for juvenile specimens, especially those of species having direct value to man. Although only the results of the 1973 study have been reported here, a preliminary, less-extensive study conducted at the same site in July and September of 1971 revealed the same basic types of differences that are described herein.

From the standpoint of coastal fisheries operations, the major detrimental effect of the thermal effluent is to decrease the suitability of the habitat for juveniles of species used by man as food and related fishery products. In the thermally affected creeks, both the numbers and the biomass of juveniles of utilizable species were 3- to 10-fold smaller than those encountered in the ambient temperature creek. Regarding these species, our data clearly show that whereas the creek receiving the largest input of thermal effluent affords a nursery habitat dominated almost entirely by

mullet (primarily *Mugil curema*), the creek functioning at ambient temperature affords a nursery habitat for a much greater array of utilizable species. In both of the thermally affected creeks there was a marked diminution in the numbers and the biomass of the following seven species of utilizable fishes (listed in order of decreasing abundance in ambient temperature creek): tidewater silverside *Menidia beryllina*, spot *Leiostomus xanthurus*, Atlantic menhaden *Brevoortia tyrannus*, silver perch *Bairdiella chrysura*, Atlantic thread herring *Opisthonema oglinum*, Atlantic croaker *Micropogon undulatus*, and pinfish *Lagodon rhomboides*.

The shallow-water habitats afforded by marshland creeks are especially important to estuarine fishes during the hot season. As shown by McErlean et al. (1973), both the number of species and the number of individuals that rely on the shallow shore zone of the estuary are maximal in summer and spring. This is due in part to the time of spawning in many species, frequently in late winter or in the spring, and to the subsequent immigration into estuarine areas of juveniles of the many transient species. The September decline in both the number and the biomass of fishes that occurred in the ambient temperature creek (Browns Creek) is similar to the fall decline described by McErlean et al. for shallow-water stations in the Patuxent River.

In the review by Wurtz and Renn (1965) on water temperature and aquatic life, the following statements were made: "Although there are historic records of fish surviving natural temperatures of 100°F, this is unusual. Waters with temperatures that regularly exceed 95°F would not be expected to support a large, or diverse, fish population." It is noteworthy that throughout the period of this study, June through September, daily temperatures in San Carlos Creek routinely exceeded 95°F (35°C). In July and September, the average daytime temperatures recorded at all stations in this creek were, with but one exception, greater than 95°F (see Table 1). A maximum temperature of 102.6°F (39.2°C) was recorded at one station in July. Although the overall population of fishes found in San Carlos Creek was neither large nor very diverse, 15 species exhibited no marked diminution in numbers, and a few species were actually more abundant here than in the ambient temperature creek. Among the species of temperature tolerant fishes recorded in the current study, the gray snapper was reported by Nugent (1970) as being a species whose numbers were not diminished by the thermal effluent of a power plant situated to the south of Miami. Although the gray snapper was the most abundant species collected in the gill net samples reported by Nugent, it was a very minor member of the fish population sampled in our study. Nugent also reported that the tarpon, *Megalops atlantica*, was equally abundant at both heated and control stations. In the current study large tarpon were seen during midsummer within a few hundred yards of the outfall of the power plant in San Carlos Creek although no specimens were collected. Nugent reported a decrease in the numbers of white mullet (primarily adults taken by gill nets) at stations in the area of elevated temperature during the hot season. In the current study the estimated density of juvenile white mullet was quite similar in all of the creeks. Trembley (1961) reported that mummichogs from the Delaware River, acclimated to 32.2°C, had an LD_{50} (mean lethal dose) of 39.4°C. If this LD_{50} approximates that in our own study area then the presence of large numbers of this species in San Carlos Creek indicates that it is literally thriving in an environment in which the temperatures encountered daily during July are very close to the upper limits for survival.

The current study was directed primarily at an analysis of the effects of a thermal effluent and related conditions upon the population of juvenile fishes utilizing a nursery habitat during the hot season. It might be contended that the effects described herein for juvenile fishes do not necessarily apply to the population of adult fishes using the same heated creeks. However, de Silva (1969) surveyed literature relating to differential tolerances exhibited by both juveniles and adults of several species. He concluded that many juveniles appear to tolerate eurythermal conditions, while adults tend to be broadly stenothermal. If the above generalization is correct, then one would predict that the effect of the thermal effluent on the population of adult fishes would be even more extreme during the hot season than the effects we recorded regarding the juvenile fishes.

We recognize that some of the population changes ascribed to elevated water temperatures in the current study may be due in part to other factors operating in concert with temperature. As was pointed out by Mihursky and Kennedy (1967), temperature tolerance limits of aquatic organisms are affected by a number of other variables such as

dissolved oxygen and carbon dioxide, salinity, and a variety of toxic substances. The St. Johns River in the vicinity of Jacksonville receives a multitude of pollutants in addition to thermal effluent. It is impossible to quantify the relative role played by other pollutants in altering the fish populations in the thermally affected creeks. However, since our control creek (Browns Creek) probably received the same array of extraneous pollutants from the river as did the heated creeks, it is possible to use the fish population found in Browns Creek as an indicator of how the system is faring without the addition of the thermal effluent and the various chemicals associated with power plant operation.

It is not the intent of this report to criticize the Northside Generating Station or the Jacksonville Electric Authority for the effects that the operation of their power plant is having upon the nursery area capacity of the adjacent marshland. It is realized that this plant is operating within the guidelines dictated by appropriate State and Federal agencies. Further, it is recognized that the acreage of marshland affected by this plant represents only a minute portion of the total marshland habitat available in this area. However, it is the intent of this report to show that massive discharges of thermal effluent do have a very obvious detrimental effect on the capacity of an estuarine receiving water to continue functioning as a nursery area for a variety of important species. This particular detrimental effect has received inadequate attention in the past. Since nursery areas represent one of our most valuable estuarine resources, it is imperative that this resource and its impairment should be given proper consideration during the site selection stages that precede the construction of future power plants.

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ADDITIONAL STUDIES OF THE FISHES, MACROINVERTEBRATES, AND HYDROLOGICAL CONDITIONS OF UPLAND CANALS IN TAMPA BAY, FLORIDA

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ABSTRACT

Hydrological and biological data from a concluding study of upland canals in Tampa Bay, Fla., are presented and compared with those collected the previous year. Critically low levels of dissolved oxygen occurred more frequently and over a longer period of time in the second year. Most affected were the inland portions of the canal system where the number of species declined markedly over the previous year. Impoverishment of fauna on or near the bottom is expected to recur during summer months because of oxygen depletion resulting from a combination of continuing accumulation of decomposing organic sediment, warm water, and little circulation in the dead-end canals.

In order to create waterfront property while not violating legislation that curtails dredging and filling of wetlands below the mean high-water line, land developers in Florida and elsewhere are digging access canals that lead from open water to upland acreage (Barada and Partington 1972). Florida's shoreline has already been extensively altered by such practice (McNulty et al. 1972), and further alteration can be expected because of ever-increasing demand for waterfront property. If the coastal zone is to be managed wisely, information on the suitability of these man-made waterways as habitat for aquatic organisms is urgently needed.

In June 1970 a small, upland canal system in Old Tampa Bay, Fla., was completed (Figure 1). This offered a unique opportunity to study the development of and changes in ecological conditions in upland canals. The fishes, macroinvertebrates, and hydrological conditions occurring in the canals during the first year following completion of the system were described by Lindall et al. (1973). In that study, however, the unusual occurrence of red tide (caused by *Gymnodinium breve*) and drought produced conditions that were atypical for the area. Conditions during our second year were more typical. Further studies by us are unlikely owing to closure of the laboratory at St. Petersburg Beach and relocation of personnel. Thus, we present the results from our follow-up study in this paper. We discuss the hydrological conditions and biota found in the canals during the second year and make comparisons with those found in the first year.

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STUDY AREA AND METHODS

The study area, known as Tanglewood Estates, is located on the southwest shore of Old Tampa Bay in northeast St. Petersburg, Fla. (Figure 1). Development of the canal system, sampling procedures, sampling gear, and station descriptions were reported previously (Lindall et al. 1973). Briefly, sampling consisted of trawling at each station in the canals with concomitant measurements of temperature, salinity, and oxygen. Sampling was conducted monthly from October 1971 through September 1972.

TEMPERATURE

Water temperatures at the control and canal stations are shown in Figure 2. At the control station (Station 1) surface and bottom temperatures ranged from 20.0° to 29.3°C and were nearly identical in any one sampling period. The greatest difference was in December when the bottom was 1.1°C higher than the surface. Canal stations showed greater temperature ranges than the control station. They ranged from 20.0° to 30.6°C at the surface and 17.8° to 29.7°C at the bottom. With few exceptions, water temperature at the bottom

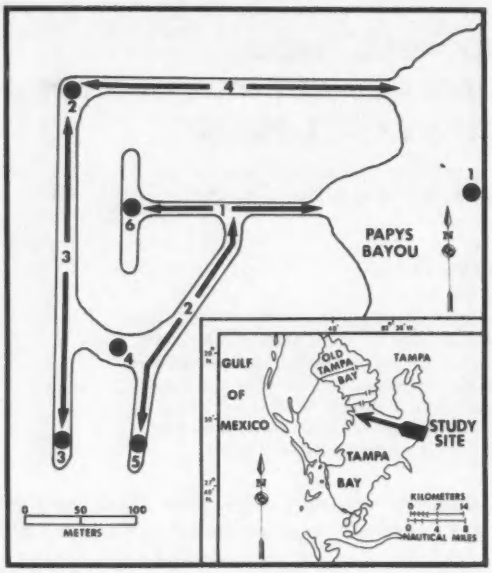

FIGURE 1.—Tampa Bay, Fla., showing location of study area and sampling stations (hydrologic station • ; trawl station ⟷).

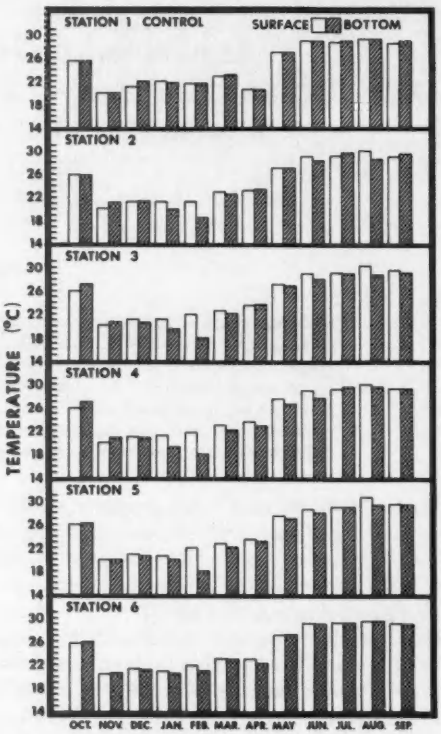

FIGURE 2.—Monthly water temperature at the surface and bottom of all hydrologic stations, October 1971-November 1972.

of the canals was lower than at the surface in any one sampling period. A definite thermocline was noted in January and February with the most inland stations exhibiting the greatest differences between surface and bottom temperatures. The greatest difference was at Station 5 in February when the bottom was 4.0°C lower than the surface.

In the previous year's study, the greatest difference was at Station 4 (February 1971) when the bottom was 1.8°C lower than at the surface (Lindall et al. 1973).

SALINITY

Surface and bottom salinities at the control station ranged from 19.1 to 28.0‰ during the study and were nearly identical in any one sampling period (Figure 3). The greatest difference was in May when the bottom was 0.7‰ lower than the surface. Surface salinities at canal stations were similar to those at the control station, ranging from 19.1 to 28.5‰. With few exceptions, however, salinity at the bottom of the canals was higher than at the surface in any one sampling period. The greatest difference was at Station 3 in October when the bottom was 4.5‰ higher than the surface.

Stratification of salinity was also noted in the previous year's study (Lindall et al. 1973). Differences between surface and bottom were not as pronounced during most of that study because drought conditions prevailed throughout most of the year. Heavy rains in August 1971 ended the drought. Thus, greater differences between surface and bottom salinities (as much as 15‰) were recorded in the previous study than in the present study.

OXYGEN

Dissolved oxygen levels at each station are shown in Figure 4. Only at the control station were surface and bottom values similar, differing no more than 0.3 ml/liter in any one sampling period. At this station the lowest observed concentration was 2.2 ml/liter (July 1972). Surface oxygen values in the canals ranged from 2.4 to 6.2 ml/liter and were similar to those at the control station throughout the year. Oxygen at the bottom

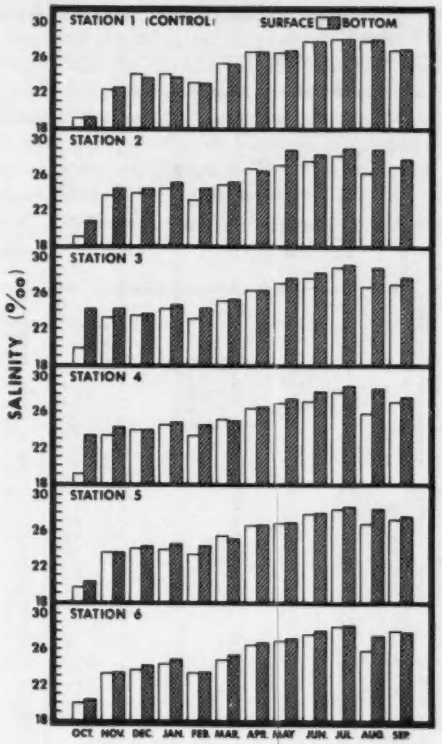

FIGURE 3.—Monthly salinity at the surface and bottom of all hydrologic stations, October 1971-November 1972.

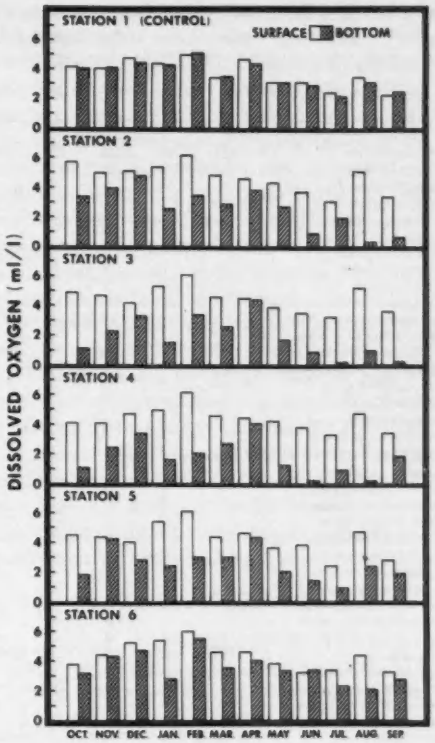

FIGURE 4.—Monthly dissolved oxygen at the surface and bottom of all hydrologic stations, October 1971-November 1972.

of the canals was always less than at the surface with the single exception of Station 6 in June. Moreover, about 50% of the bottom samples taken throughout the year at stations farthest from the bayou (Stations 3-5) contained less than 2.0 ml/liter of oxygen; several were anoxic or nearly so. At Station 6, closest to the bayou, oxygen levels were never observed to be less than 2.1 ml/liter. Trent et al. (1972) also reported oxygen depletion at inland portions of housing development canals in Galveston Bay, Tex., during the summer.

Results of the previous year's study showed severe oxygen depletion in the canals during the summer months following a red tide (caused by *Gymnodinium breve*) outbreak (Lindall et al. 1973). In that study decaying fish killed by the red tide placed additional oxygen demand on the system and precluded the determination of the extent to which dissolved oxygen would have been depressed in the absence of red tide. In the present study, no red tide occurred, but oxygen was again depleted at the bottom of the most inland stations in the canals during the summer. In fact, low dissolved oxygen occurred more frequently and over a longer period of time (October 1971 and May through September 1972) than in the previous year.

FISHES AND MACROINVERTEBRATES

Thirty-eight species and 9,502 individuals of vertebrates and invertebrates were collected in the canals during the year (Table 1). Of the 38 species, 34 were finfish, 1 was the diamondback terrapin, *Malaclemys terrapin*, and 3 were commercially important invertebrates (blue crab, *Callinectes sapidus*; pink shrimp, *Penaeus duorarum*; and brief squid, *Lolliguncula brevis*). Fourteen of the 34 species of finfish did not occur in the previous year's catch. These 14 species, however, made up less than 1% of the total catch.

TABLE 1—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at all stations from October 1971 through September 1972.

Species	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Total	
													No.	%
Vertebrates:														
Anchoa mitchilli	429	1,360	3,368	1,516	296	360	0	1,005	42	6	22	449	8,853	93.2
Anchoa hepsetus	0	0	0	0	0	0	0	208	1	0	1	0	210	2.3
Bairdiella chrysura	0	0	19	0	0	0	4	29	41	1	1	0	95	1.1
Chaetodipterus faber	0	0	9	0	0	0	1	1	16	5	1	1	34	0.5
Syngnathus scovelli[1]	0	0	0	0	4	1	0	7	5	0	0	0	17	0.2
Lagodon rhomboides	0	0	0	0	0	2	6	3	3	0	0	0	14	0.1
Gobiosoma bosci	0	1	1	0	2	4	0	2	3	0	0	0	13	0.1
Pogonias cromis	0	0	1	1	0	2	8	0	0	0	1	0	13	0.1
Lucania parva[1]	0	0	1	1	2	2	0	4	0	0	0	0	10	0.1
Diapterus plumieri[1]	0	0	4	0	2	0	0	0	0	0	2	1	9	0.1
Eucinostomus argenteus	0	0	7	1	0	0	0	1	0	0	0	0	9	0.1
Menticirrhus americanus	0	1	0	0	0	0	0	5	0	2	1	0	9	0.1
Cynoscion arenarius	0	0	0	0	0	0	0	3	0	1	2	2	8	0.1
Orthopristis chrysoptera	0	0	0	0	0	0	4	1	0	0	0	0	5	0.1
Eucinostomus gula	0	0	0	0	0	0	0	0	4	0	0	0	4	0.1
Trinectes maculatus[1]	0	0	4	0	0	0	0	0	0	0	0	0	4	0.1
Cynoscion nebulosus	0	0	0	0	0	0	0	3	0	0	0	0	3	0.0
Microgobius gulosus	0	0	0	0	0	0	0	0	0	1	1	1	3	0.0
Opisthonema oglinum	0	0	0	0	0	0	1	2	0	0	0	0	3	0.0
Sciaenops ocellata	0	0	1	1	1	0	0	0	0	0	0	0	3	0.0
Sphoeroides nephelus	0	2	0	0	1	0	0	0	0	0	0	0	3	0.0
Chilomycterus schoepfi[1]	0	0	0	0	0	0	0	1	1	0	0	0	2	0.0
Epinephelus itajara[1]	0	0	0	1	0	0	0	0	0	1	0	0	2	0.0
Gobiosoma robustum[1]	0	0	0	0	0	1	0	1	0	0	0	0	2	0.0
Hippocampus erectus[1]	0	0	0	0	1	0	0	0	0	0	1	0	2	0.0
Leiostomus xanthurus	0	0	0	0	0	2	0	0	0	0	0	0	2	0.0
Malaclemys terrapin	0	0	0	0	0	0	0	0	1	0	0	1	2	0.0
Monacanthus hispidus[1]	0	0	0	0	0	1	0	1	0	0	0	0	2	0.0
Syngnathus louisianae[1]	0	0	0	0	0	0	0	1	0	1	0	0	2	0.0
Archosargus probatocephalus	0	0	0	0	0	0	0	0	1	0	0	0	1	0.0
Arius felis	0	0	0	0	0	0	0	0	0	0	1	0	1	0.0
Elops saurus[1]	0	0	0	0	1	0	0	0	0	0	0	0	1	0.0
Harengula pensacolae[1]	0	0	0	0	0	0	0	1	0	0	0	0	1	0.0
Hippocampus zosterae[1]	0	0	0	0	0	0	0	0	0	1	0	0	1	0.0
Lactophrys quadricornis[1]	0	0	0	0	0	0	0	0	0	1	0	0	1	0.0
Invertebrates:														
Lolliguncula brevis	0	0	1	0	1	11	7	17	21	13	0	15	86	0.9
Callinectes sapidus	0	4	11	8	5	4	10	2	3	0	1	1	49	0.5
Penaeus duorarum	0	1	5	6	1	0	0	1	1	3	3	2	23	0.2
Total species	1	6	13	8	12	11	8	22	14	12	13	9	38	
Total individuals	429	1,369	3,432	1,535	317	390	41	1,299	143	36	38	473	9,502	100.0

[1]Did not occur in catches from August 1970 through August 1971 (Lindall et al. 1973).

The four species of finfish caught in greatest abundance represented 97% of the total number of specimens (Table 1). They were the bay anchovy, *Anchoa mitchilli*; striped anchovy, *A. hepsetus*; silver perch, *Bairdiella chrysura*; and Atlantic spadefish, *Chaetodipterus faber*. The bay anchovy alone accounted for more than 93% of the total number caught.

In the previous year's study (Lindall et al. 1973) the four dominant species of fish, representing 92% of the catch, were bay anchovy (7,557 individuals—72%); spotfin mojarra, *Eucinostomus argenteus* (921 individuals—8.8%); spot, *Leiostomus xanthurus* (821 individuals—7.8%); silver jenny, *Eucinostomus gula* (372 individuals—3.5%). The latter three species combined consisted of only 15 individuals in the present study and made up only 0.2% of the catch (Table 1). Each of these three species is a bottom feeder (Darnell 1958; Springer and Woodburn 1960; Carr and Adams 1973), and the prolonged period of low dissolved oxygen at the bottom of the canals probably accounted for the 99% reduction in their numbers.

The brief squid was the most abundant invertebrate (54% of all invertebrates collected) and made up about 1% of all animals collected during the year. Based on the previous year's catch, the number of squid in the canal system declined by about 78%, while the total numbers of pink shrimp and blue crab remained about the same.

Of the 38 species collected during the year, most occurred at Station 4 (28 species), followed by Station 1 (21 species), Station 3 (18 species), and Station 2 (14 species). Compared with the previous year, the number of species collected at Stations 1 and 4 were about the same, but those at Stations 2 and 3 declined markedly (30% and 50% respec-

tively). We were not surprised to find fewer species at Stations 2 and 3, because these stations are farthest from the bayou and were most affected by the critically low oxygen levels. As evidence, catches at the four trawl stations during the summer period of low dissolved oxygen (July-August) are compared in Figure 5. The vast majority of species and individuals occurred nearest the bayou (Stations 1 and 4) during this period of stress.

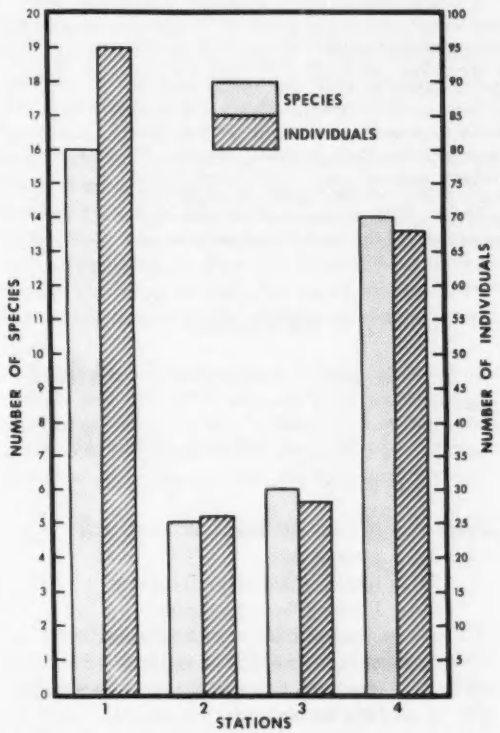

FIGURE 5.—Number of species and individuals caught at each trawl station during the summer period of low dissolved oxygen (June through August 1972).

CONCLUSIONS

The upland canal system known as Tanglewood Estates is poorly designed with respect to providing year-round, quality habitat for estuarine species of fish and shellfish. Apparently caused by prolonged periods of low dissolved oxygen at the bottom of the canals, the numbers of squid (*Lolliguncula brevis*) and three species of finfish (*Eucinostomus argenteus*, *E. gula*, and *Leiostomus xanthurus*) were drastically reduced in the second year of the system's existence. We believe that the ability of the canal system to provide adequate oxygen for respiration of bottom-dwelling fishes is becoming progressively worse. The main causative factors are: 1) lack of water exchange with the adjacent bayou, 2) water depths greater than the depth of the photic zone, thus preventing photosynthesis by benthic flora, and 3) continuing accumulation of decomposing soft sediments (Hall and Lindall[4]).

The major advantages of upland canal development, as opposed to bayfill development, are that bay bottom is not adversely altered and water circulation patterns are not altered significantly. In fact, estuarine area is increased. However, as long as land developers continue to design upland canals with dead ends and excessive depths, oxygen depletion and the resulting impoverishment of fauna on or near the bottom can be expected to be a recurring problem in summer months.

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A REEVALUATION OF THE COMBINED EFFECTS OF TEMPERATURE AND SALINITY ON SURVIVAL AND GROWTH OF BIVALVE LARVAE USING RESPONSE SURFACE TECHNIQUES

R. GREGORY LOUGH[1]

ABSTRACT

The combined effects of temperature and salinity on larval survival and growth of *Crassostrea virginica*, *Mercenaria mercenaria*, and *Mulinia lateralis* as reported in the literature were critically examined using response surface techniques. The late veliger larvae generally have a greater tolerance to both temperature and salinity than the developing embryos. Each species shows its own characteristic change in temperature-salinity tolerance as it develops and approaches the range normally tolerated by the adults as it matures. Maximum growth of the veliger larvae required higher temperatures and somewhat higher salinities than maximum survival. Differences in temperature-salinity ranges estimated for maximum survival and growth were significantly different for all three species. In each case growth showed a significant temperature-salinity interaction. Response surface plots are given for early larval survival and late veliger survival and growth. Inferences of tolerance studies are made to the fields of pollution and aquaculture.

Recent studies of the combined effects of temperature and salinity on early development of bivalve larvae have been done by Davis and Calabrese (1964) for *Crassostrea virginica* and *Mercenaria mercenaria*, Brenko and Calabrese (1969) for *Mytilus edulis*, Calabrese (1969) for *Mulinia lateralis*, Lough and Gonor (1971, 1973a, b) for *Adula californiensis*, and Goodwin (1973) for *Panope generosa*. However, only Lough and Gonor (1973a, b) have critically examined the effects of temperature and salinity on bivalve larval life by multiple regression analyses and the fitting of response surfaces to survival, growth, and respiration of early and late stage larvae. The use and evaluation of this response surface technique in marine ecology has been reviewed in detail by Alderdice (1972). This technique not only facilitates the prediction of an organism's response to a wide range of untested conditions but also visually represents any change in its response at various stages of development. The experimental data from the above mentioned species have been critically analyzed by response surface techniques to reevaluate the combined effects of temperature and salinity on larval survival and growth. The results for *Crassostrea virginica*, *Mercenaria mercenaria*, and *Mulinia lateralis* are given in this paper.

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METHODS

The mathematical model used in the analyses was of the form:

$$Y = b_0 + b_1 (T) + b_2 (S) + b_3 (T^2) + b_4 (S^2) + b_5 (T \times S)$$

where Y = percentage survival or growth
b_0 = a constant
T = linear effect of temperature
S = linear effect of salinity
T^2 = quadratic effect of temperature
S^2 = quadratic effect of salinity
$T \times S$ = interaction effect between temperature and salinity

The coefficients in the model (b's) were estimated by a stepwise multiple regression computer program contained in the Oregon State University Statistical Program Library. F-levels were set equal to zero to enter and remove variables. This allowed all variables to come into the equation by a forward selection process, their order of insertion determined by using the partial correlation coefficient as a measure of their importance. The contribution a variable makes in reducing the variance of the equation can also be considered by looking at the various values given as the program proceeds. One of the more useful is the square of the multiple correlation

coefficient, R^2, defined as the sum of squares due to regression divided by the total sum of squares corrected for the mean. It is often stated as a percentage, $100R^2$. The larger R^2 is, the better the fitted equation explains the variation in the data. Values of R^2 can be compared at each stage of the regression program. A t-test also is made indicating the equality of the individual regression coefficients to zero and their level of significance.

The calculated regression coefficients from a particular equation were fitted by computer to a full quadratic equation in temperature and salinity in order to print a contour diagram of the response surface. The computer program was instructed to print 20% contour intervals, wide enough to exclude the approximate ±10% experimental error reported by the authors. Temperature and salinity scales on all plots were set to range from 0 to 40 in order to facilitate response comparison and to allow the overall form of the surface to be visualized. Contours extrapolated beyond the experimental data are given as dotted lines.

Analysis of covariance methods, as used in Lough and Gonor (1973a, b), were used to test the significance of the difference between the estimated polynomials for early and late larval survival and between late survival and growth.

RESULTS

Crassostrea virginica

Davis and Calabrese (1964) first reared the larvae for 2 days at six levels of temperature and nine levels of salinity to study the effect of these factors on early development, or the period from fertilization to approximately the veliger stage. To learn what effect these same combinations of temperature and salinity had on late larval development, larvae were initially reared from eggs for 2 days at normal seawater conditions (24.0°C, 27.5‰) and then transferred at the veliger stage to the experimental conditions.

Tables of the multiple regression analyses are given in the Appendix and will not be referred to in this section. Survival to 2 days of development was affected most by the linear and quadratic effects of salinity and the linear effect of temperature. Maximum survival of the 2-day-old larvae (80% survival contour) was estimated to occur at temperature and salinity conditions between 19° and 30.5°C and 19 and 30‰ (Figure 1), which is in good agreement with the experimental results.

The analysis of survival of 10-day-old larvae, after 8 days of rearing at experimental conditions, indicated that the linear and quadratic effects of temperature and the quadratic effect of salinity significantly affected survival. Maximum survival after 8 days (60% survival contour) was estimated to occur above 21°C and between 8 and 30.5‰ (Figure 2). The 10-day-old larvae showed a tolerance to much higher temperature and a wider salinity range than the 2-day-old larvae. Analysis of covariance showed a significant difference (1% level) between the 2- and 8-day survival polynomials further substantiating that the range of temperatures and salinities tolerated by the late veliger larvae were significantly different than that of the early embryos.

Growth of the larvae during 8 days was affected most by the interacting effect of temperature and salinity and the quadratic effect of salinity. Maximum growth (100% response contour) was estimated to occur at temperatures and salinities above 19°C and 33‰ (Figure 3).

There was a significant difference (1% level) between the polynomials estimated for 8-day

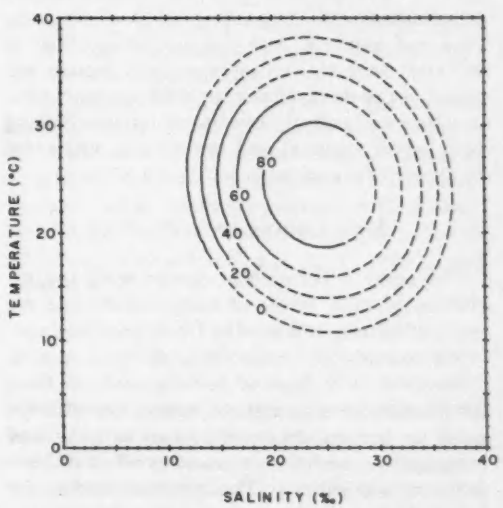

FIGURE 1.—Response surface estimation of percent survival of *Crassostrea virginica* larvae after 2 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

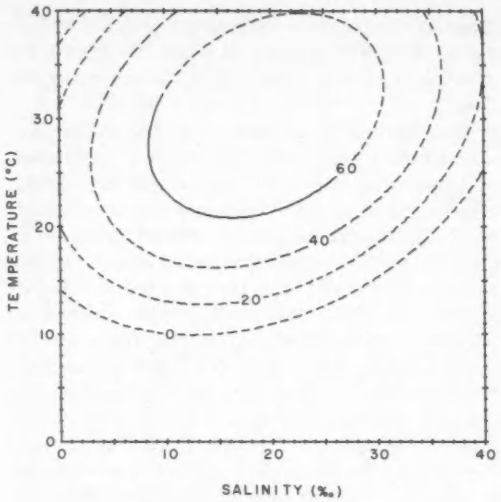

FIGURE 2.—Response surface estimation of percent survival of *Crassostrea virginica* veliger larvae after 8 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

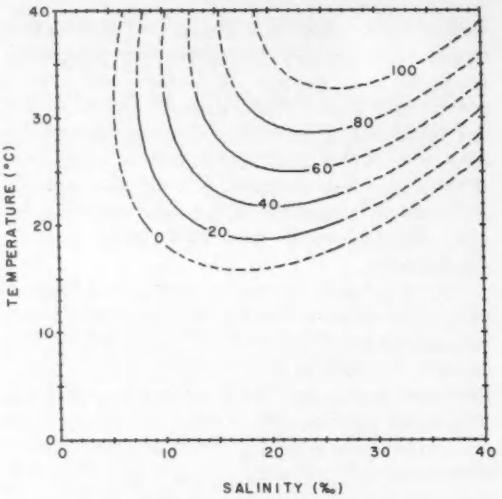

FIGURE 3.—Response surface estimation of percent growth of *Crassostrea virginica* veliger larvae after 8 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

survival and growth indicating a significantly higher salinity range is required for optimum growth than is required for optimum survival.

An analysis of combined 8-day-survival and growth data indicated that the linear effect of temperature, the interacting effect of temperature and salinity, and the quadratic effect of salinity were the more important factors explaining the data. Optimum (80% contour) temperature and salinity conditions for maximizing both larval survival and growth was estimated at above 30°C and between 18 and 35‰.

Mercenaria mercenaria

The same experimental design with the exception of nine levels of temperature and six levels of salinity was used by Davis and Calabrese (1964) to study the larval tolerance of this species.

Survival to 2 days of development, or from fertilization to veliger stage larvae, was affected most by the quadratic effects of salinity and temperature, and the interacting effect of temperature and salinity. The response surface for 2-day-old larvae clearly shows the skewed contours resulting from the interaction effect (Figure 4). Maximum survival to 2 days of development (100% survival contour) was estimated to occur at temperatures and salinities above 7.2°C and 28‰. Their experimental data show maximum survival between 17.5° and 30°C at a salinity of 27‰.

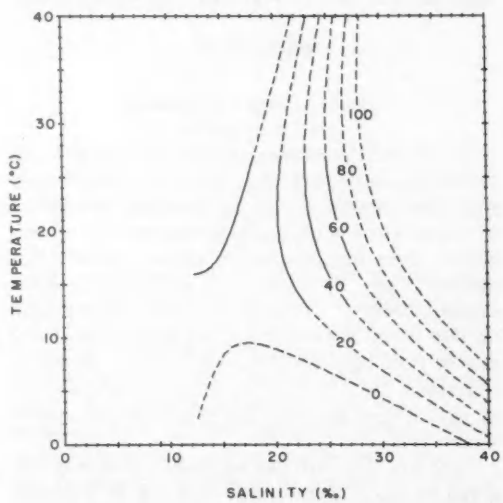

FIGURE 4.—Response surface estimation of percent survival of *Mercenaria mercenaria* larvae after 2 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

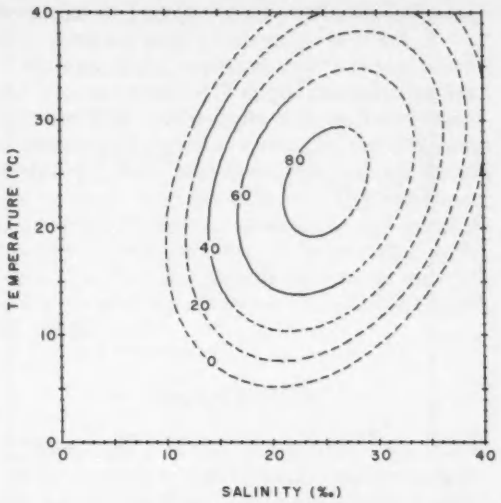

FIGURE 5.—Response surface estimation of percent survival of *Mercenaria mercenaria* veliger larvae after 10 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

Late larval survival after 10 days of rearing at the experimental conditions indicated that the linear and quadratic effects of salinity and the interacting effect of temperature and salinity were the more important factors affecting survival. Maximum survival of these 12-day-old larvae (80% survival contour) was estimated to occur between temperatures and salinities of 19° and 29.5°C and 21 and 29‰ (Figure 5). Although the late larvae had a much narrower temperature tolerance than the developing embryos, the late larvae showed a significantly greater tolerance to low salinity. This difference in tolerance of these two life stages was further substantiated by the fact that there was a significant difference (1% level) between the 2- and 10-day survival polynomials.

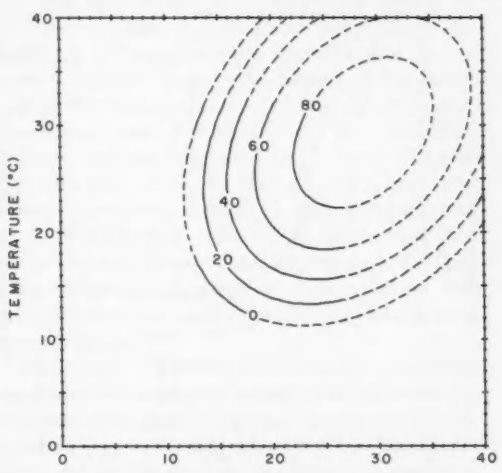

FIGURE 6.—Response surface estimation of percent growth of *Mercenaria mercenaria* veliger larvae after 10 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

Growth of the larvae during the 10-day experimental period was most affected by the interacting effect of temperature and salinity and by the linear and quadratic effects of temperature, and the linear effect of salinity. Maximum growth (80% contour) was estimated to occur at temperatures and salinities between 22.5° and 36.5°C and 21.5 and 30‰ (Figure 6). There was a significant difference (1% level) between the polynomials estimated for 10-day survival and growth indicating that the higher temperatures and salinities required for optimum growth are significantly different than those conditions estimated for optimum survival. Larval survival and growth estimated by these techniques above the experimental temperature and salinity of 32.5°C and 27.0‰ are questionable. Higher temperature and salinity levels need to be added to the experimental design to more carefully define the response surface.

The combined 10-day survival and growth analysis indicated that they were affected by all of the variables of temperature and salinity, but by salinity more than by temperature. Optimum temperature and salinity conditions (80% contour) for maximizing both larval survival and growth to 12 days was estimated at 21.5° to 33°C and 22 to 31‰.

Mulinia lateralis

Six levels each of temperature and salinity were used to investigate the tolerances of early and late development of this species by Calabrese (1969) in the same manner as used for the other species.

Survival of the early embryos for 2 days under the experimental conditions was affected by all the variables except the interacting effect of

temperature and salinity. Maximum survival of the 2-day-old larvae (80% contour) was estimated to occur at temperatures between 18.5° and 24.5°C and salinities between 22 and 28.5‰ (Figure 7).

The analysis of survival after 6 to 8 days of rearing beyond the veliger stage indicated that the linear and quadratic effects of temperature and the interacting effect of temperature and salinity were the more important variables affecting survival. Response surface estimation predicted 80% survival at temperatures between 8.5° and 26.5°C and salinities above 12‰ (Figure 8). A significant difference (1% level) was calculated by the analysis of covariance for the 2- and 6- to 8-day survival polynomials. The veliger larvae showed a much greater tolerance to low temperatures and a wider range of salinities than the early embryos.

Growth of the veliger larvae was most affected by the interacting effect of temperature and salinity, the quadratic effect of salinity, and the linear effect of temperature. Maximum growth (60% contour) was estimated to occur at temperatures between 18° and 38°C and salinities above 16.5‰ (Figure 9). The axis of the growth contours are observed to lie diagonal to the factor axes showing the effect of the temperature-salinity interaction. There was a significant (1% level) difference between the polynomials estimated for the 6- to 8-day survival and growth indicating that the higher temperatures required

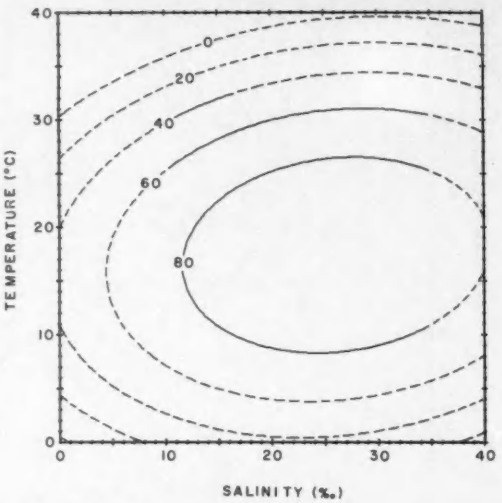

FIGURE 8.—Response surface estimation of percent survival of *Mulinia lateralis* veliger larvae after 6 to 8 days of development at experimental temperature and salinity combinations given in Calabrese (1969).

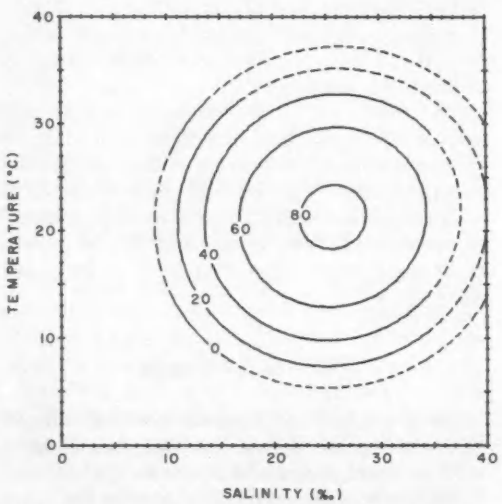

FIGURE 7.—Response surface estimation of percent survival of *Mulinia lateralis* larvae after 2 days of development at experimental temperature and salinity combinations given in Calabrese (1969).

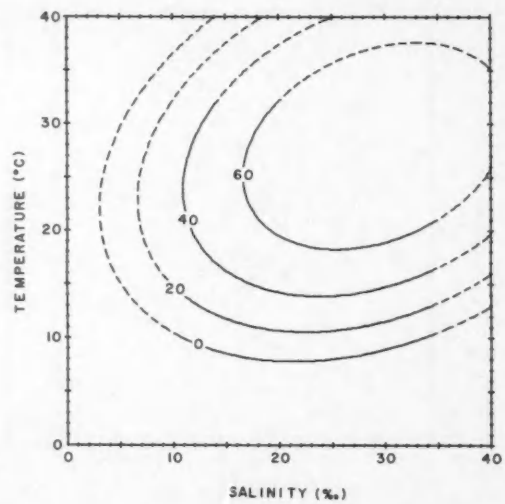

FIGURE 9.—Response surface estimation of percent growth of *Mulinia lateralis* veliger larvae after 6 to 8 days of development at experimental temperature and salinity combinations given in Calabrese (1969).

for optimum growth were significantly different than those required for optimum survival.

Analysis of the combined 6- to 8-day survival and growth indicated that the interacting effect of temperature and salinity and the linear effect of temperature were the more important variables explaining the data, although only 30.4% of the variance was explained by the combined polynomial. Optimum temperature and salinity conditions (80% contour) for maximizing both larval survival and growth to 8 to 10 days of age were predicted between 20° and 26°C and 23 and 32‰.

DISCUSSION

Despite the fact that the adults of the three species studied are euryhaline to varying degrees, their early embryos and larvae have a comparatively narrow salinity range. Early larvae of *Mercenaria mercenaria* appear to be much more tolerant to high temperatures than the other two species, but require essentially oceanic salinities.

The older larvae, having been reared from fertilization to the veliger stage at optimum conditions, now appear to have a generally greater tolerance to both temperature and salinity. The late larvae of *C. virginica* appear to tolerate a higher temperature range than the early larvae while *Mulinia lateralis* late larvae seem to tolerate best temperatures at the lower end of its range. Late larvae of *Mercenaria mercenaria* are able to tolerate low salinities somewhat better than the early larvae, but their temperature range is quite restricted. The observed progressive change in their temperature-salinity tolerance with time approaches the range normally tolerated by the adults. This same progressive change was observed for the larvae of *Adula californiensis* by Lough and Gonor (1973a, b).

The range of temperature-salinity conditions estimated for maximum growth was significantly different from that estimated for maximum survival of the same late stage larvae. Maximum predicted growth occurred at higher temperatures and at somewhat higher salinities than those for maximum survival for all three species studied. All three species showed a significant temperature-salinity interaction effect for growth. Growth, classically, is positively correlated with temperature up to some limit; however, the role of salinity appears to complicate the temperature effect.

The combining of late larval survival and growth to maximize both responses seems intuitively pleasing as one would expect a compromise situation in nature. An organism probably can operate most effectively when it is in a set of environmental conditions which maximize all its biological responses. It has been shown by Lough and Gonor (1973a, b) that temperatures for maximum growth response may be an abnormal stress environment which ultimately results in high mortality. Similarly, low temperatures may be suitable for larval survival but not necessarily highly productive for recruitment and growth to the adult population. Although the optimum temperatures and salinities usually can be estimated from the raw data, the statistical techniques used in this study allow one to define and interpret an organism's response to a matrix of environmental factors and to determine whether the response(s) between stages of development or sampling intervals is significantly different.

INFERENCES

Tolerance studies of various stages or at various times in the life history of an organism are especially important to pollution studies. Different stages of crab larvae have been shown to have different temperature-salinity tolerances of ecological significance (Costlow et al. 1960, 1962, 1966). This study demonstrates that different periods in the life of bivalve larvae also differ in their tolerance to temperature and salinity. The determination of water quality standards based on only one stage in the life of an organism is not realistic. All stages of development are important, particularly when the synergistic effect of a pollutant is studied. Davis and Hidu (1969) found it was necessary to evaluate the effects of pesticides on all stages of clam and oyster larvae as their tolerances are markedly different.

The field of aquaculture also may benefit from these tolerance studies. Based on this study a long-term experimental program should be undertaken to maximize both survival and growth recognizing that different stages of an organism may have different optimum conditions. Possibly,

larvae should be reared at one set of conditions from fertilization to veliger stage and then transferred to another set of conditions for the late stages. Juvenile clams may have yet another set of optimum conditions different than those of the late larval stage. The larvae and the adults are two distinct morphological and physiological organisms and occupy distinctly different ecological environments.

Recent work by Costlow and Bookhout (1971) on the cyclic effect of temperatures on the larval development of an estuarine mud crab, *Rhithropanopeus harrisii*, emphasizes the need for more research on the fluctuating environmental variables that normally occur in nature. The possible stimulating or inhibiting effect of fluctuating temperatures on bivalve larval survival and growth in relation to both pollution and aquaculture should be investigated in the future.

ACKNOWLEDGMENT

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APPENDIX

APPENDIX TABLE 1.—Multiple regression analyses of *Crassostrea virginica* larvae.

Step number	Variable	R^2	*F*-level	df	Level of significance	Coefficient	*T*-value	Level of significance
				2-day survival				
1	S	0.661	77.857	(1,40)	1%	32.8617	8.007	1%
2	S^2	.793	24.818	(2,39)	1%	−0.6234	6.706	1%
3	T^2	.795	.356	(3,38)	N.S.	−0.5195	5.715	1%
4	T	.889	31.397	(4,37)	1%	27.7755	5.821	1%
5	$T \times S$	.894	1.875	(5,36)	N.S.	−0.0971	1.369	N.S.
	Constant					−643.9149		
				8-day survival				
1	T	0.426	38.600	(1,52)	1%	10.221	2.992	1%
2	T^2	.493	6.781	(2,51)	1%	−0.2006	3.008	1%
3	$T \times S$	.501	.778	(3,50)	N.S.	0.0996	2.492	5%
4	S^2	.625	1.612	(4,49)	N.S.	−0.1455	3.687	1%
5	S	.643	2.430	(5,48)	N.S.	2.6621	1.559	N.S.
	Constant					−104.389		
				8-day growth				
1	$T \times S$	0.642	93.200	(1,52)	1%	0.2450	6.645	1%
2	S^2	.907	144.539	(2,51)	1%	−0.2329	6.401	1%
3	S	.918	7.139	(3,50)	1%	4.1512	2.636	5%
4	T	.919	.317	(4,49)	N.S.	7.5246	2.389	5%
5	T^2	.927	5.365	(5,48)	1%	−0.1425	2.316	5%
	Constant					−152.2672		
				8-day survival and growth				
1	T	0.431	80.437	(1,106)	1%	8.8727	2.182	5%
2	$T \times S$	.528	21.559	(2,105)	1%	0.1723	3.620	1%
3	S^2	.602	19.110	(3,104)	1%	−0.1892	4.028	1%
4	T^2	.619	4.587	(4,103)	1%	−0.1715	2.160	5%
5	S	.629	2.807	(5,102)	5%	3.4066	1.676	N.S.
	Constant					−128.3283		

APPENDIX TABLE 2.—Multiple regression analyses of *Mercenaria mercenaria* larvae.

Step number	Variable	R^2	*F*-level	df	Level of significance	Coefficient	*t*-value	Level of significance
				2-day survival				
1	S^2	0.561	43.513	(1,34)	1%	0.2439	0.611	N.S.
2	$T \times S$	.581	1.555	(2,33)	N.S.	0.3947	2.345	5%
3	T^2	.640	5.223	(3,32)	1%	−0.1219	2.039	N.S.
4	T	.648	.678	(4,31)	N.S.	−2.7229	0.819	N.S.
5	S	.653	.449	(5,30)	N.S.	−12.2188	0.670	N.S.
	Constant					110.3864		
				10-day survival				
1	S	0.488	49.560	(1,52)	1%	15.6884	4.021	1%
2	S^2	.594	13.307	(2,51)	1%	−0.4142	4.570	1%
3	T^2	.609	1.894	(3,50)	N.S.	−0.2630	4.916	1%
4	$T \times S$	.732	22.546	(4,49)	1%	0.2111	3.295	1%
5	T	.769	7.591	(5,48)	1%	7.4766	2.755	1%
	Constant					−201.8315		
				10-day growth				
1	$T \times S$	0.631	88.900	(1,52)	1%	0.2438	4.532	1%
2	T^2	.739	31.109	(2,51)	1%	−0.3305	7.262	1%
3	T	.829	36.270	(3,50)	1%	12.3631	5.363	1%
4	S^2	.841	3.706	(4,49)	5%	−0.3702	4.835	1%
5	S	.885	18.518	(5,48)	1%	14.0885	4.303	1%
	Constant					−288.6339		
				10-day survival and growth				
1	S	0.463	91.215	(1,106)	1%	14.5902	4.532	1%
2	S^2	.535	16.411	(2,105)	1%	−0.3876	5.164	1%
3	$T \times S$	.590	13.881	(3,104)	1%	0.2316	4.378	1%
4	T^2	.685	31.236	(4,103)	1%	−0.2987	6.719	1%
5	T	.736	19.522	(5,102)	1%	9.9556	4.418	1%
	Constant					−243.0117		

APPENDIX TABLE 3.—Multiple regression analyses of *Mulinia lateralis* larvae.

Step number	Variable	R^2	*F*-level	df	Level of significance	Coefficient	*t*-value	Level of significance
				2-day survival				
1	S	0.156	6.269	(1,34)	5%	14.4237	4.949	1%
2	S^2	.390	12.705	(2,33)	1%	−0.2942	4.916	1%
3	$T \times S$	.421	1.708	(3,32)	N.S.	0.0264	0.554	N.S.
4	T^2	.478	3.359	(4,31)	5%	−0.3256	5.440	1%
5	T	.709	23.769	(5,30)	1%	13.1265	4.875	1%
	Constant					−240.8807		
				6- to 8-day survival				
1	T^2	0.353	18.540	(1,34)	1%	−0.1976	7.190	1%
2	T	.627	24.193	(2,33)	1%	6.0749	4.914	1%
3	$T \times S$	.716	10.002	(3,32)	1%	0.0307	1.305	N.S.
4	S^2	.724	.898	(4,31)	N.S.	−0.0781	2.843	1%
5	S	.760	7.013	(5,30)	1%	3.5437	2.648	5%
	Constant					−2.8961		
				6- to 8-day growth				
1	$T \times S$	0.498	33.698	(1,34)	1%	0.0993	2.646	5%
2	S^2	.605	8.979	(2,33)	1%	−0.1258	2.867	1%
3	T^2	.641	3.220	(3,32)	5%	−0.2120	4.833	1%
4	T	.765	16.222	(4,31)	1%	8.9352	4.528	1%
5	S	.796	4.584	(5,30)	1%	4.5735	2.141	5%
	Constant					−113.4013		
				6- to 8-day survival and growth				
1	$T \times S$	0.102	7.963	(1,70)	1%	0.0650	1.438	N.S.
2	T^2	.120	1.408	(2,69)	N.S.	−0.2048	3.876	1%
3	T	.262	13.046	(3,68)	1%	7.5051	2.377	1%
4	S^2	.278	1.491	(4,67)	N.S.	−0.1020	1.930	N.S.
5	S	.304	2.489	(5,66)	5%	4.0586	1.578	N.S.
	Constant					−58.1487		

SWIM-BLADDER STATE AND STRUCTURE IN RELATION TO BEHAVIOR AND MODE OF LIFE IN STROMATEOID FISHES

MICHAEL H. HORN[1]

ABSTRACT

Fourteen of the 15 genera of stromateoid fishes possess a relatively small (0.6-3.4% of body volume), euphysoclistous swim bladder which forms early in life (3-5 mm standard length) and regresses in all genera except possibly *Nomeus* before maturity (150-200 mm standard length) is reached. The organ is thus an almost exclusive characteristic of the juveniles which occupy surface layers (upper 100-150 m) in coastal and oceanic waters.

The gas gland of the swim bladder consists of cuboidal to irregularly shaped cells 6-46 μm in greatest dimension. The retia mirabilia range in length from 0.4 to 2.0 mm and in diameter of individual capillaries from 4 to 10 μm. The area of the gas gland and the length of the retia relative to the size of the swim-bladder lumen are great compared to the same in other epipelagic fishes and are similar to those of deeper living, mesopelagic fishes. The relatively large gas-secreting complex is considered to be an adaptation for rapid and efficient gas secretion in maintaining hydrostatic equilibrium as the juvenile fishes swim in the surface layers, frequently in association with floating objects, where pressure changes are greatest with depth.

Swim-bladder loss accompanies changes in behavior and mode of life and is part of the transition from the juvenile to the adult stage of life. Hovering and high maneuverability as principal components of locomotor behavior in juveniles give way to continuous swimming in adults which are generally independent of floating objects and occupy a greater depth range. The relative length of the paired fins changes with age and varies among the species. *Peprilus triacanthus* and *P. simillimus*, negatively buoyant, active swimmers, have long pectoral fins as adults whereas *Schedophilus medusophagus*, a neutrally or nearly neutrally buoyant, slow-moving fish, has short pectoral fins. Both *P. simillimus* and *S. medusophagus* have high levels of lipid which may serve to replace the swim bladder in a buoyancy function when the fishes are adults.

The swim bladder (or gas bladder), a gas-filled organ unique to bony fishes, has its greatest functional significance as a hydrostatic device, i.e., one that provides neutral or nearly neutral buoyancy to the fish. It is one of the most plastic of vertebrate organs (Marshall 1960) and occurs in a great diversity of fishes from a variety of habitats. The swim bladder is not necessary for life as it is absent in many fishes, but according to Fänge (1966) about one-half of the 20,000 existing species have it as adults and even more as larvae or juveniles. The organ, owing to its diversity of form and widespread occurrence, should reflect in its presence or absence and structure the behavior and mode of life of the fishes possessing it. In stromateoid fishes, the swim bladder regresses in 13, possibly 14, of the 15 genera, and the regression seems to be associated with other morphological changes and changes in mode of life (Horn 1970a).

The swim bladder of stromateoid fishes has received little mention in the literature partly due to its absence or reduced state in adults. Goode and Bean (1895) and Jordan and Evermann (1896) stated that the organ was "usually absent" in the Stromateidae, and the former as well as Grey (1955) reported its absence in the Tetragonuridae. Fowler (1936) in his treatment of several stromateoid genera indicated that the swim bladder was "present or absent." Goode and Bean (1895) stated that it was present in *Nomeus* as did Haedrich (1967) for *Ariomma*. Based upon an examination of approximately one-half of the species in the group, I have found the organ to be present at some stage (larval and/or juvenile) in the life of all stromateoid genera except *Pampus*. Even in *Pampus* it may be present at an early stage since larvae or small juveniles (< 20 mm SL, standard length) were not studied.

The perciform suborder Stromateoidei consists of 6 families, 15 genera, and about 60 species (Haedrich and Horn 1972) and is characterized by toothed saccular outgrowths in the gullet and by

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small teeth approximately unilateral in the jaws (Haedrich 1967). The larvae and juveniles occur mainly in the surface layers of the ocean and are frequently associated with animate or inanimate floating objects. The adults, ranging in maximum size from about 30 to 120 cm, form a diverse group of temperate and tropical species which variously occupy a wide range of depths in coastal and oceanic waters (including mesopelagic and bathypelagic levels). The Centrolophidae (six genera) are either coastal or oceanic, the Stromateidae (three genera) are coastal, the Amarsipidae (one genus), Nomeidae (three genera), and Tetragonuridae (one genus) are oceanic, and the Ariommidae (one genus) are benthopelagic on the continental shelf and slope.

The purposes of the present paper are to 1) describe the morphology and histology of the stromateoid swim bladder, 2) compare the dimensions and capabilities of the stromateoid swim bladder with that of other fishes of similar and different habitats, and 3) discuss the relationship of swim-bladder state and structure to the behavior and mode of life of stromateoids based upon the results of the present and other studies.

MATERIALS AND METHODS

The majority of specimens examined (Table 1) for swim-bladder structure and other morphological detail were preserved although fresh or frozen material of several species was studied. Observations on the behavior of certain species were made and are briefly described in appropriate sections of the paper.

Specimens in addition to those personally collected were obtained from the following institutions: British Museum (Natural History), London; Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; Institute of Oceanographic Sciences, Wormley, England; Natural History Museum of Los Angeles County, Los Angeles, Calif.; Scripps Institution of Oceanography, La Jolla, Calif.; Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla; Woods Hole Oceanographic Institution, Woods Hole, Mass.; and Zoological Museum, Copenhagen, Denmark.

Swim-bladder dimensions were measured with an ocular micrometer in either a dissecting or compound microscope or, in large specimens, with dial calipers. Swim-bladder and body volumes were determined by displacement and/or, for the former, calculated on the assumption that the bladder was a prolate spheroid ($v = 4/3\pi ab^2$, where a and b are the major and minor semiaxes (see Capen 1967)). Volume measurements were made from swim bladders that were in most cases well expanded. Ten percent was allowed for shrinkage of preserved material.

Transverse or longitudinal serial sections of the swim bladder of 13 genera and species were cut at 8-μm thickness and stained with haemalum and eosin.

Buoyancy determinations were made by weighing each fish in air and in water of known temperature and salinity. Results are expressed as the percentage of the air weight that each fish weighed in seawater.

TABLE 1.—Stromateoid specimens examined for swim bladder and other morphological characteristics.

Family and species	Number of specimens	Size range (mm SL)
Centrolophidae:		
Hyperoglyphe antarctica	4	23.4- 34.9
Hyperoglyphe perciformis	2	35.8, 47.7
Schedophilus huttoni	1	22.9
Schedophilus maculatus	2	70.2, 77.5
Schedophilus medusophagus	7	10.4-285.0
Centrolophus maoricus	3	15.1-127.8
Centrolophus niger	2	124.0, 231.0
Icichthys lockingtoni	20	3.5-268.0
Seriolella punctata	2	132.0, 162.6
Seriolella violacea	3	12.8- 84.0
Psenopsis cyanea	2	94.2, 104.2
Stromateidae:		
Stromateus brasiliensis	7	75.7-167.3
Stromateus fiatola	9	12.5- 93.5
Stromateus stellatus	5	17.5- 99.4
Peprilus burti	3	57.4- 95.1
Peprilus paru	10	28.6-123.0
Peprilus simillimus	17	2.0-135.0
Peprilus triacanthus	10	12.0-120.4
Pampus argenteus	7	24.6- 49.0
Pampus chinensis	6	25.4- 67.3
Amarsipidae:		
Amarsipus carlsbergi	3	22.0- 67.5
Nomeidae:		
Cubiceps caeruleus	1	18.5
Cubiceps carinatus	1	8.5
Cubiceps gracilis	10	16.5-330.0
Nomeus gronovii	13	11.6-142.7
Psenes arafurensis	2	17.0, 18.0
Psenes cyanophrys	17	9.1-120.0
Psenes maculatus	1	33.6
Psenes pellucidus	2	26.9, 34.8
Unidentified (probably *Psenes*)	5	3.4- 12.3
Tetragonuridae:		
Tetragonurus cuvieri	13	4.0-242.0
Ariommidae:		
Ariomma bondi	7	20.9-124.3
Ariomma indica	1	59.7
Ariomma melanum	2	each 134.1
Ariomma regulus	3	123.3-150.0
Ariomma sp. (either *A. bondi* or *A. melanum*)	1	16.5
Total number of specimens	204	

RESULTS

Swim-Bladder Structure

The stromateoid swim bladder is of the physoclistous, two-chambered type usually found in perciform fishes (Horn 1970a) (Figure 1). The delicate, thin-walled sac lies in the upper part of the body cavity above the gut and below the kidney and is closely invested by the dorsal peritoneum. A muscular diaphragm (not always visible) divides the bladder into anterior and posterior chambers (Figures 1, 2), the latter of which serves a gas-resorbing function (a euphysoclistous condition). The gas gland, associated with the anterior chamber, typically forms a U-shape and may be single or divided into two or more lobes (Figure 1). Cells composing the gland are cuboidal to irregular in shape and usually in two or more layers (Figures 2-5). Some cells appear to be either syncytial or of the giant type found widely distributed in marine euphysoclists (Fänge 1953) and in some deep-sea fishes (Marshall 1960). The retia mirabilia are unipolar,

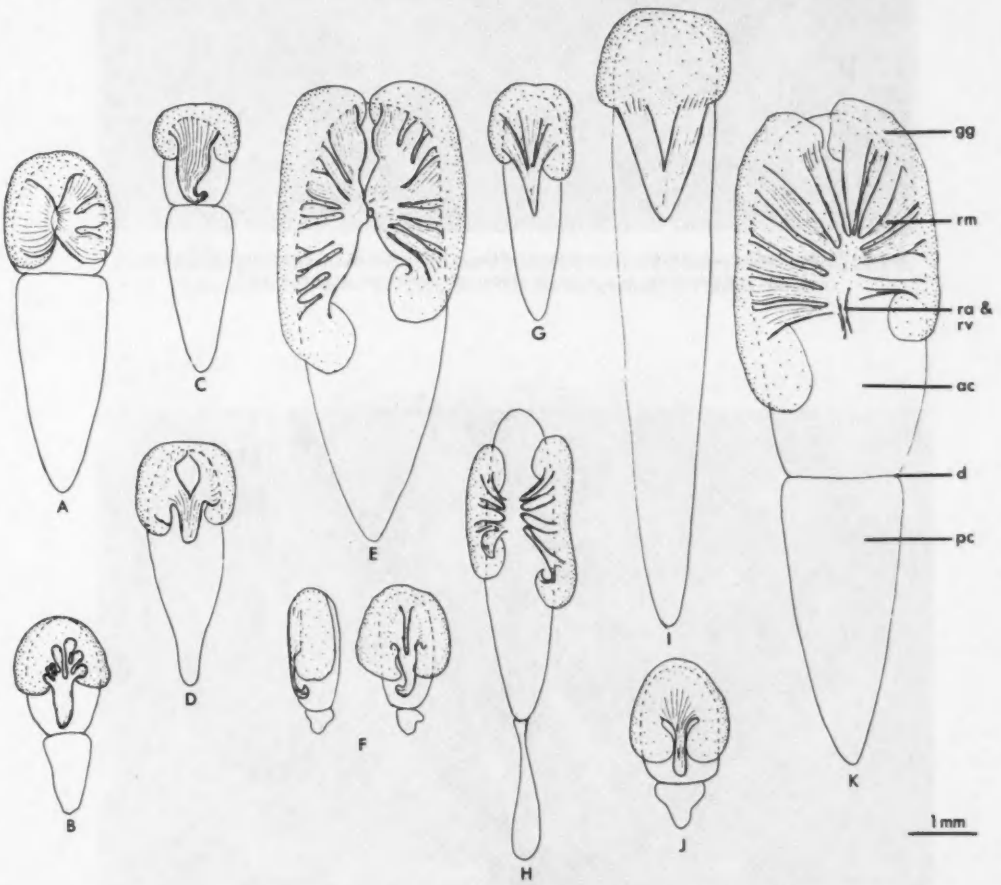

FIGURE 1.—Ventral view of the swim bladder of 11 species of stromateoids (all drawn to same scale). **gg**, gas gland (slightly flattened and expanded); **rm**, rete mirabile; **ra** and **rv**, retial artery and retial vein; **ac**, anterior chamber; **d**, diaphragm; **pc**, posterior chamber. **A**, *Ariomma bondi*, 24.2 mm SL; **B**, *Centrolophus maoricus*, 15.1 mm SL; **C**, *Tetragonurus cuvieri*, 28.8 mm SL; **D**, *Seriolella violacea*, 12.8 mm SL; **E**,*Cubiceps gracilis*, 30.5 mm SL; **F**, *Schedophilus medusophagus*, 17.4 mm SL (lateral and ventral view); **G**, *Psenes cyanophrys*, 11.5 mm SL; **H**, *Nomeus gronovii*, 26.4 mm SL; **I**, *Stromateus fiatola*, 34.1 mm SL; **J**, *Icichthys lockingtoni*, 16.3 mm SL; **K**, *Hyperoglyphe antarctica*, 34.9 mm SL.

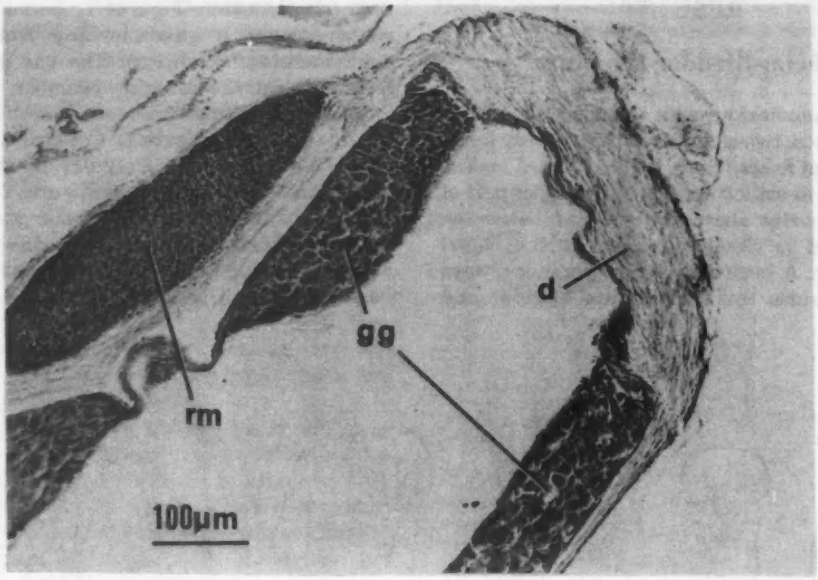

FIGURE 2.—Sagittal section of the anterior chamber of the swim bladder of *Ariomma bondi*. d, diaphragm; gg, gas gland; rm, rete mirabile. (From same specimen as Figure 1A.)

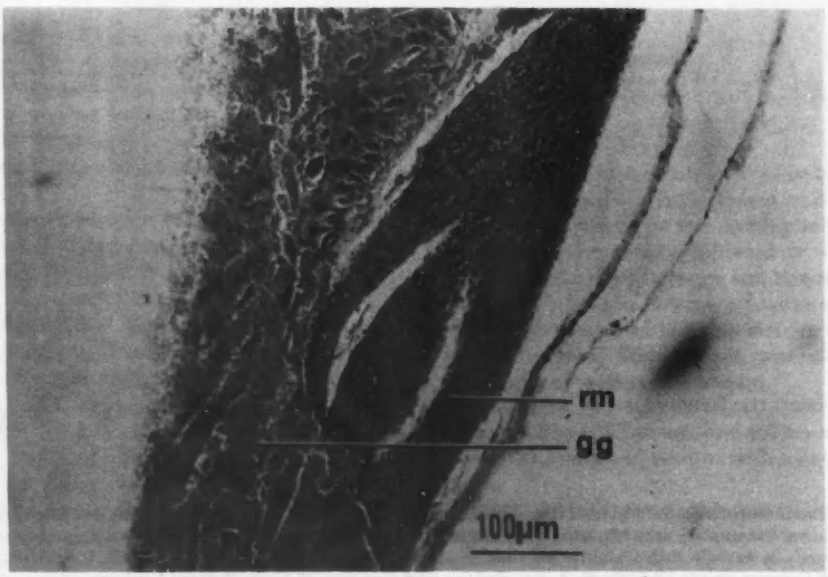

FIGURE 3.—Sagittal section of the gas secreting complex of the swim bladder of *Cubiceps gracilis*. gg, gas gland; rm, rete mirabile. (From same specimen as Figure 1B.)

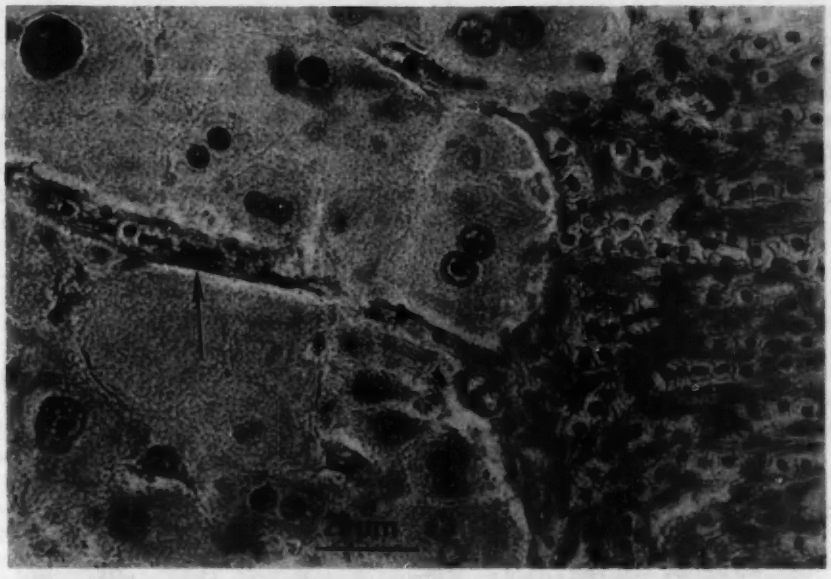

FIGURE 4.—Gas gland cells and retial capillaries of the swimbladder of *Cubiceps gracilis*. Arrow points to retial capillary between gas gland cells. (From same specimen as Figures 1E and 3.)

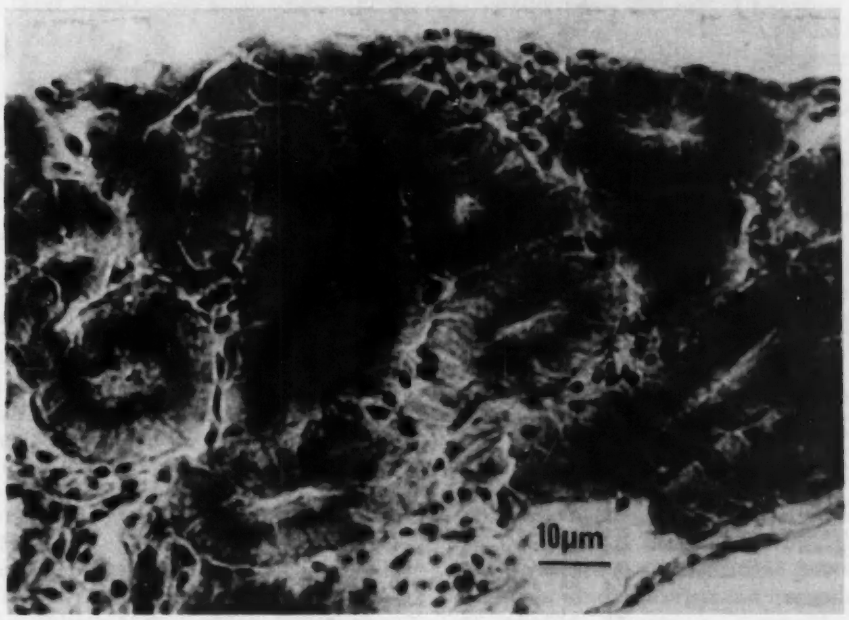

FIGURE 5.—Gas gland of *Peprilus triacanthus*, 16.5 mm SL, showing arrangement of cells. (Transverse section.)

i.e., the artery and vein subdivide to form parallel capillaries which enter the gas gland (Figures 3, 4, 6). Retial orientation varies from a position parallel to the long axis of the swim bladder to one that is perpendicular (Figure 1). Size characteristics of swim-bladder components are given in Table 2. Distinctive features of the swim bladder of the six stromateoid families are described below.

Centrolophidae

Swim-bladder volume in the fishes examined varied from less than 1% of body volume in *Schedophilus* to greater than 3% in *Hyperoglyphe*. Size (greatest dimension) of the gas gland cells ranged from 10-17 μm in *Hyperoglyphe* and *Seriolella* to 20-40 μm in *Schedophilus*. Retial length ranged from 1.1 mm in *Seriolella* to 2.0 mm

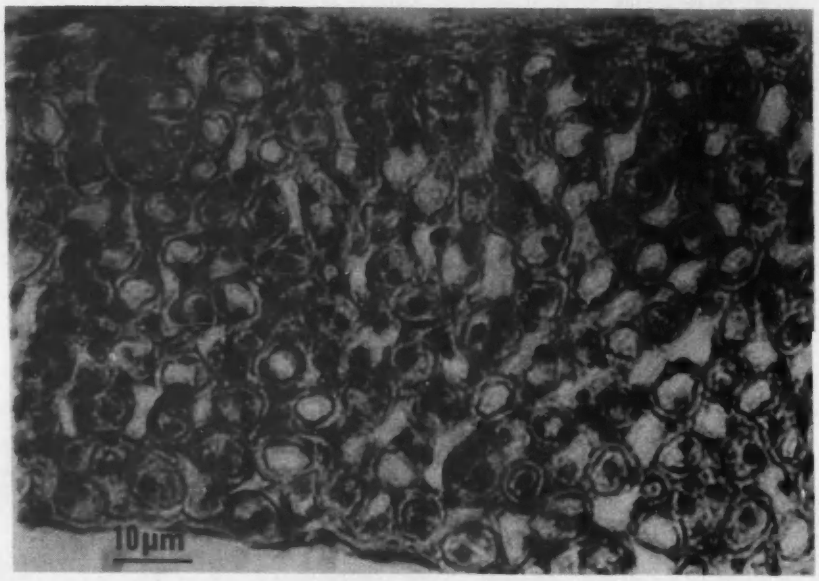

FIGURE 6.—Transverse section through the rete mirabile of the swim bladder of *Tetragonurus cuvieri*. (From same specimen as Figure 1C.)

TABLE 2.—Size characteristics of the swim-bladder lumen, gas gland, and rete mirabile in 12 species of stromateoids.

		Lumen			Gas gland		Rete mirabile			
Species	Size (mm SL)	L × W (mm)	Vol (mm^3)	Vol (%)	Area (mm^2)	Cell size (μm)	Capillary diam (μm)	Length (mm)	Total number of capillaries	Total capillary length (m)
Hyperoglyphe antarctica	34.9	9.8 × 2.7	37.0	3.4	5.4	10-17	7-10	1.3-2.0	2,000	2.6 -4.0
Schedophilus medusophagus	17.4	2.1 × 0.8	—	—	1.8	20-40	8-10	1.3	800	1.04
Icichthys lockingtoni	16.3	2.4 × 1.2	2.0	3.0	2.1	15-20	6-8	1.4	1,000	1.4
Seriolella violacea	12.8	3.5 × 1.1	—	—	1.0	10-17	4-8	1.1-1.2	1,200	1.3 -1.4
Stromateus fiatola	34.1	9.1 × 2.0	—	—	2.9	10-20	6-8	1.8-2.0	1,500	2.7 -3.0
Peprilus triacanthus	16.5	2.5 × 1.0	3.0	2.3	0.8	6-10	5-6	0.8	600	0.48
Amarsipus carlsbergi	22.0	2.0 × 0.8	0.7	—	1.0	8-20	4-8	0.7-0.9	1,100	0.77-0.99
Cubiceps gracilis	30.5	6.6 × 2.3	21.0	3.3	8.7	25-40	8-10	1.1-1.9	3,000	3.5 -5.7
Nomeus gronovii	26.4	6.7 × 1.0	3.5	0.7	1.6	—	—	0.4-0.6	—	—
	27.4	6.8 × 1.3	—	—	2.5	10-30	5-6	0.5-0.6	2,000	1.0 -1.2
Psenes cyanophrys	14.1	3.7 × 1.2	2.5	2.1	0.7	—	—	1.0	—	—
	18.6	5.1 × 1.6	—	—	6.0	25-40	5-6	0.8-0.9	1,500	1.2 -1.35
Tetragonurus cuvieri	28.8	3.8 × 1.0	2.0	0.6	0.6	8-20	4-10	1.3	1,000	1.3
Ariomma bondi	23.3	6.5 × 1.3	7.0	2.9	3.6	—	—	0.9	—	—
	24.2	5.0 × 1.4	5.0	1.7	3.7	20-46	8	0.6-0.9	2,500	1.5 -2.25

in *Hyperoglyphe*. Retial orientation was generally parallel to the long axis of the bladder, and the retial bundle either remained single anteriorly as in *Icichthys* (Figure 1J) or variously branched into smaller bundles perpendicular to the long axis as in *Hyperoglyphe* (Figure 1K). The rete bundle of *Schedophilus* had a sharp turn near the posterior end producing a sigmoid outline (Figure 1F). Swim-bladder shape which depends to a large degree upon secretory and absorptive states varied from elongate with a large posterior chamber to short and bulbous with either a small posterior chamber or no posterior chamber visible.

Stromateidae

The organ was similar in structure and shape to that of the Centrolophidae. The gas gland cells of *Peprilus triacanthus* were small (6-10 μm) and were arranged in loops and rings (Figure 5). In one *P. triacanthus* (16.5 mm SL) the retial blood vessels formed a single bundle posteriorly which expanded anteriorly over the gas gland whereas in two somewhat larger juveniles (22.2 and 33.9 mm SL) the retia were more nearly perpendicular to the long axis of the bladder and consisted of 7 or 8 distinct branches.

Amarsipidae

The swim bladder was similar to that of the Centrolophidae. The rete originated posteriorly as a single bundle and divided anteriorly into 7 or 8 distinct branches before entering the gas gland.

Nomeidae

Swim-bladder volume ranged from 0.7% in *Nomeus* to 3.3% of body volume in *Cubiceps* and gas gland size from 10-30 μm in *Nomeus* to 25-40 μm in *Cubiceps* and *Psenes*. Retial length varied from 0.4 mm in *Nomeus* to 1.9 mm in *Cubiceps*. The retia were divided into several branches and in position were more nearly perpendicular than parallel to the long axis of the bladder (Figure 1E, H). Small juvenile *Psenes cyanophrys* (9.1 and 14.1 mm SL) had retia almost parallel to the long axis of the bladder (Figure 1G) whereas larger juveniles (e.g., 60.8 mm SL) tended to have retia which were more nearly perpendicular to the long axis and more highly branched. The pattern, seen also in *Peprilus triacanthus*, may be part of the regression process that the swim bladder undergoes.

Tetragonuridae

The sac was small (0.6% of body volume) and elongate. The retial bundle was parallel to the long axis of the bladder and, as in *Schedophilus medusophagus*, had an S-shaped turn near the posterior end (Figure 1C). The gas gland was relatively small and located at the anterior end of the lumen.

Ariommidae

The swim bladder was relatively large (up to 2.9% of body volume) and elongate. The gas gland cells were in the upper range of size (20-46 μm) among the stromateoids examined, and the retia were broad, fanlike and perpendicular to the long axis of the bladder (Figure 1A).

Size at Swim-Bladder Inflation

The swim bladder becomes functional early in the life of stromateoids. Whether the larval fishes gulp air at the surface or whether gas is secreted to initially fill the bladder was not determined. Examination of larvae of four genera indicated that the organ in one species was almost completely developed at 3.0 mm SL and in three others at slightly larger sizes. Specimens of *Peprilus simillimus* as small as 3.0 mm SL had what appeared to be a fully developed swim bladder whereas in smaller individuals, e.g., 2.7 mm SL, the sac was inflated but the gas gland and retia were incomplete. The bladder was absent in a fish of 2.4 mm SL. A series of larvae, 3.4-5.0 mm SL, of an unidentified species of *Psenes* had an inflated swim bladder, and larvae of *Tetragonurus cuvieri* as small as 4.0 mm SL had a gas-filled sac which was visible through the semitransparent body wall. Individuals of *Icichthys lockingtoni*, 5.0 and 7.5 mm SL, had an inflated sac and an apparently fully developed gas gland and retial complement.

Swim-Bladder Regression

The swim bladder regresses, becomes nonfunctional, and finally disappears before the adult stage is reached in all stromateoid genera except *Pampus* in which the organ is apparently absent and possibly *Nomeus* in which the largest individual examined (142.7 mm SL) had a functional swim bladder. The regression is a

TABLE 3.—Surface area of the gas gland (mm^2) and length of the rete mirabile (mm) relative to swim-bladder volume (mm^3 or ml) or dimension (length × width, in mm) in the European eel, certain shallow-sea and deep-sea fishes, and in 12 species of stromateoids. Total capillary length (m) = retial length × number of retial capillaries. Retial lengths of stromateoids are means of individuals for each species.

Species	Size (mm SL)	Gas gland area × 1,000/swim-bladder volume (mm^3)	Retial length × 1,000/swim-bladder dimension	Total capillary length/swim-bladder volume (ml)
European eel[1]				
Anguilla anguilla	—	—	—	30
Shallow-sea (epipelagic):[1]				
Cypsilurus cyanopterus	290.0	8	0.5	—
Danichthys rondeletii	214.0	8	1.3	—
Exocoetus volitans	159.0	6	5	—
Petalichthys capensis	—	—	1.5	—
Hyporhamphus sp.	112.0	40	8	—
Scomberesox saurus	—	—	2	—
Gadus minutus	—	—	13	—
Capros aper	—	—	18	—
Deep-sea:[1]				
Gonostoma denudatum	81.0	—	76	—
Pollichthys mauli	43.0	—	125	—
Bonapartia pedaliota	67.0	—	71	—
Vinciguerria attenuata	43.5	140	34	—
Vinciguerria nimbaria	—	—	—	150
Argyropelecus aculeatus	23.0	140	38	50
Polyipnus laternatus	36.0	—	143	100
Astronesthes niger	41.0	250	111	—
Astronesthes similis	104.0	170	—	—
Myctophum punctatum	71.0	200	40	20
Benthosema suborbitale	24.0	500	—	—
Lampanyctus guntheri	53.0	330	142	—
Diaphus rafinesquei	—	—	21	—
Melamphaes megalops	56.0	60	250	30
Stephanoberyx monae	83.5	—	63	—
Chiasmodon niger	104.0	250	71	—
Stromateoids:				
Hyperoglyphe antarctica	34.9	140	63	89
Schedophilus medusophagus	17.4	—	1,000	—
Icichthys lockingtoni	16.3	1,000	500	700
Seriolella violacea	12.8	—	333	—
Stromateus fiatola	34.1	—	100	—
Peprilus triacanthus	16.5	250	333	167
Amarsipus carlsbergi	22.0	—	500	—
Cubiceps gracilis	30.5	500	100	214
Nomeus gronovii	26.4	500	77	—
Psenes cyanophrys	11.5	1,000	333	—
Tetragonurus cuvieri	28.8	330	333	650
Ariomma bondi	23.3	500	111	380

[1]Data from Marshall (1960).

gradual process which makes difficult the determination of the exact time of loss of function. Several stages are recognizable in the process although they vary in appearance, and both the stages and the overall regression vary in duration among and within species. Estimated ranges of fish size during which regression occurs in nine stromateoid species are given in Table 4.

Early in the regression the gas gland contracts and thickens and the sac begins to decrease in size. Later the gas gland and retia mirabilia become atrophied as the cells and capillaries lose integrity (Figure 7). A yellowish-white material, possibly lipid, frequently invests the gas gland. Finally, the swim-bladder wall is resorbed, and the gas secreting and absorbing complexes become indistinct. A large stromateoid (> 100-200 mm SL, see Table 4) may have either a small irregularly shaped mass of yellowish-white material lying in the dorsal mesentery (Figure 7) as the only remnant of the swim bladder or no visible trace at all of the organ.

DISCUSSION

Relative Dimensions and Capabilities of the Swim Bladder

Volume

Mean percentage volumes were relatively small, 0.6-3.4% (Table 2), and generally below the 3.1-5.7 range for the swim bladder calculated by Alexander (1966) to be necessary for neutral buoyancy in seawater. A number of mid-water fishes also have swim bladders of low volume

TABLE 4.—Size ranges during which swim-bladder regression occurs in nine species of stromateoids and during which the same species have been observed in association with animate (mainly coelenterate) or inanimate floating objects. Former ranges derived from data of present study and latter from sources listed.

Species	Size during regression (mm SL)	Size during association (mm SL, FL, or TL)[1]	Associated species or object	Source[2]
Centrolophus niger	50-75	30-40 TL	*Rhizostoma pulmo*	Mansueti 1963
		103-477 SL	*Mola mola*	Mackay 1972
Icichthys lockingtoni	40-65	55 TL	*Pelagia noctiluca*	Mansueti 1963
		16.3 SL	*Pelagia noctiluca*	Specimen label (MCZ)
		180.5 TL	*Pelagia noctiluca*	Mansueti 1963
Stromateus fiatola	50-75	10-40 TL	*Rhizostoma pulmo*	Mansueti 1963
(including *S. fasciatus*)		10-40 TL	*Cotylorhiza tuberculata*	Mansueti 1963
		127 TL	Unidentified medusa	Mansueti 1963
		12.5-28.2 SL	*Cassiopeia carbonica*	Specimen label (ZMC)
Peprilus triacanthus	75-100	10-20 TL	*Chrysaora quinquerirrha*	Mansueti 1963
		51-64 TL	*Cyanea capillata*	Mansueti 1963
		50-73 TL	Unidentified medusa	Mansueti 1963
Peprilus paru (including	60-100	18-69 TL	*Chrysaora quinquecirrha*	Mansueti 1963
P. alepidotus)		13 TL	*Chrysaora quinquecirrha*	Mansueti 1963
		147 TL	Unidentified medusa	Mansueti 1963
		28.6 SL	Unidentified medusa	Specimen label (BMNH 1956.11.12.12)
Cubiceps gracilis	40-75	42 SL	Unidentified medusa	Specimen label (BMNH 76.6.21-2)
Nomeus gronovii	Swim bladder	20 FL	Drifting raft	Gooding and Magnuson 1967
	present	51-76 TL	*Physalia pelagica*	Mansueti 1963
	at ≥150 SL	127-152 TL	*Stomolophus meleagris*	Mansueti 1963
		142.7 SL	*Physalia pelagica*	NIO specimen, HMS *Discovery II* Stn. 6688-3
Psenes cyanophrys	110-130	15-124 FL	Drifting raft	Gooding and Magnuson 1967
(including *P. pacificus*)		10-133 SL	Flotsam	Hunter and Mitchell 1967
Tetragonurus cuvieri	40-60	34 SL	Unidentified medusa	Specimen label (BMNH 76.6.21.23)

[1]SL = standard length, FL = fork length, TL = total length.
[2]MCZ = Museum of Comparative Zoology, Harvard University.
ZMC = Zoological Museum, Copenhagen.
BMNH = British Museum (Natural History), London.

(Capen 1967; Kleckner and Gibbs 1972) and even a relatively small gas-filled sac provides some degree of buoyancy which may be significant depending upon what other lift or buoyancy devices are utilized. Larval and juvenile stromateoids, the stages which have the organ, have a different mode of life (see below) and are in some species at least probably less dense than adults. Only a 1% reduction in specific gravity of a fish lowers the required percentage volume for neutral buoyancy from 3.1%, the lower value in Alexander's (1966) calculated range (which was based upon specific gravities of adults), to 2.2% (Horn 1970a). Thus, even a small swim bladder would be an important contribution to buoyancy. Data on specific gravities of young stromateoids which might help to explain the range of percentage volumes found within the group are not yet available.

Gas Gland

The area of the gas gland relative to swim-bladder volume is similar to that in a number of deep-sea fishes and much greater than that of a series of epipelagic or shallow-sea ones (Table 3). Marshall (1960) stated that the large gas gland of deep-sea fishes, especially vertical migrators, may be an adaptation for rapid gas secretion as the fish descends. Even though juvenile stromateoids occur only in the epipelagial, the adaptive significance of a large gas gland would be the same for them as for deep vertical migrators since stromateoids range over depths in the upper 100-150 m where pressure changes are greatest (e.g., the pressure at 10 m is 2× that at the surface). Maintaining association with animate floating objects as many stromateoids do requires that fishes range, even if slowly, over depths in the surface layers and in so doing secrete gas during descents if the hydrostatic advantage of the swim bladder is to be effected. Thus, the main selective value of the large gas gland may be for making fine adjustments to buoyancy. At least some of the epipelagic fishes listed in Table 3 have a narrow vertical range near the surface and would not require as large a gas gland.

The size and structure of the gas gland cells vary widely among stromateoids, a common situation in both shallow-water (Woodland 1911; Fänge 1953) and deep-sea fishes (Marshall 1960). Cells measured in stromateoids ranged from 6 to 46 μm (Table 2), although some other cells in a few species appeared to be multinucleate and syncytial or similar to the giant cells (50-150 μm) described by Fänge (1953) and Marshall (1960). The gland consisted of relatively large cells in a

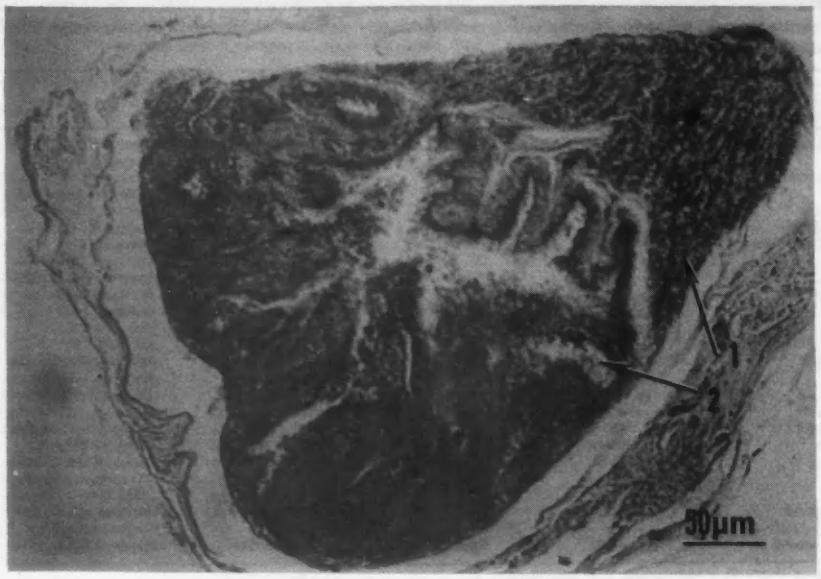

FIGURE 7.—Transverse section through the regressed swim bladder of *Ariomma indica*, 59.7 mm SL. Arrow (1) points to regressed rete mirabile, arrow (2) to regressed gas gland.

complex, multilayered arrangement as in *Ariomma bondi* (Figure 2), or, less frequently, of small cells arranged in circles or loops as in *Peprilus triacanthus* (Figure 5). The functional significance of cells of either different sizes or arrangements is poorly understood.

Rete Mirabile

Retial length in stromateoids ranged from 0.4 to 2.0 mm (Table 2), similar to the 0.75 to 2.0-mm range listed by Marshall (1972) for upper mesopelagic (200-600 m) fishes. The ratio of retial length to swim-bladder dimension (length × width) (Table 3) as an approximation of relative development is high in stromateoids and similar to that of Marshall's (1960) deep-sea group which includes some vertical migrators. The stromateoid ratio is much higher than that of other epipelagic fishes and demonstrates that the retia, as with the gas gland, which together form the gas-secreting complex, are relatively well developed in stromateoids. In addition, the total length of the retial capillaries (retial length × number of retial capillaries) in relation to swim-bladder volume is similar to or exceeds that for the eel, *Anguilla anguilla*, and certain deep-sea fishes (Table 3).

Marshall (1972) pointed out that the only flexible adaptation to increase the surface available for countercurrent gas exchange is an increase in length of the retial capillaries. An increase in length will not only lead to increased gas exchange but also slow the rate of bloodflow and so further enhance the efficiency of exchange (Marshall 1960). Marshall (1972) showed that the deeper the living space of a fish the greater the absolute length of the retia. On the basis of the pattern of retial length and depth of living described by Marshall, the predicted depth zone for larval and juvenile stromateoids would be the upper mesopelagial.

Besides length, the diameter of the retial capillaries of stromateoids shows a somewhat greater similarity to that of deep-sea fishes than to other epipelagic fishes. Stromateoids have capillary bores of 4-10 μm (Table 2) whereas epipelagic fishes listed by Marshall (1960) had diameters of greater than 10 μm. Deep-sea fishes with large erythrocytes have retial capillaries 7-18 μm in diameter and those with small, nonnucleated erythrocytes such as *Maurolicus* and *Vinciguerria* have retial capillaries 2-10 μm in diameter (Marshall 1972). The smaller the diameter the greater the efficiency of gaseous exchange (Marshall

1960), although decreased bore is an adaptation limited in most fish species by the size of the erythrocytes.

Swim-Bladder Regression in Relation to Behavior and Mode of Life

Data from the present study and other sources on depth distribution, association with floating objects, and locomotion and buoyancy make it possible to formulate a general outline of the changes in behavior and mode of life that accompany the regression of the swim bladder and which are part of the transition from the juvenile to the adult state.

Depth Distribution

Adult stromateoids generally occupy a wide range of depths either over the continental shelf or in the open ocean, whereas larvae and juveniles of all or nearly all species occur in the surface layers (mainly the upper 100 m) (Haedrich 1967, 1969; Horn 1970a). Larval nomeids (*Psenes* and *Cubiceps*) are important constituents of the epipelagic fauna; this is known especially for the eastern tropical Pacific (Ahlstrom 1971, 1972). The Centrolophidae and Tetragonuridae were listed by Ahlstrom (1969) as two of the principal families of deep-sea fishes which had larvae in the surface layers of the California Current region. The stromateid, *Peprilus simillimus*, occurs mainly in the upper 50 m of coastal waters off California and Baja California (Ahlstrom 1959), and ariommid larvae and juveniles apparently live in the surface layers although the adults are benthopelagic (Horn 1972). Thus, swim-bladder loss occurs as the fishes increase their range of vertical distribution.

Association with Floating Objects

Beginning at a small size (≤ 10 mm SL) and usually ending before maturity is reached (≤200 mm SL), stromateoids commonly associate with a wide variety of animate and inanimate floating objects (Mansueti 1963; Haedrich 1967; Horn 1970a) and during the period that the swim bladder is functional (Table 4). The associations are not obligatory but rather, as Mansueti (1963) described them, temporary ecological phenomena in which the objects (e.g., jellyfishes or flotsam) are essentially passive hosts and the fishes active opportunists. Scyphozoan medusae of several genera form a major group of associates particularly of stromateids and to some extent of centrolophids, nomeids, and tetragonurids (Mansueti 1963). The nomeid, *Nomeus gronovii*, and the Portuguese man-of-war, *Physalia*, form the apparently most intimate and enduring of "fish-jellyfish" associations. Certain stromateoids have also been found inside pelagic ascidians (Grey 1955), beneath the ocean sunfish, *Mola* (Mackay 1972) and beneath floating plants such as *Sargassum* (Haedrich 1967). Several species occur beneath flotsam, and the nomeid, *Psenes cyanophrys*, is one of the more abundant fishes under drifting objects (Hunter and Mitchell 1967, 1968; Gooding and Magnuson 1967). Drift associations are not well understood but probably provide one or more ecological advantages such as food, protection, or visual stimuli.

Juvenile stromateoids in their coloration and maneuverability are well adapted for life beneath floating objects, especially coelenterates. Young fish typically have a banded, mottled, or blotched pattern whereas adults are generally uniform in color or are dark above and pale below. The duration of the juvenile color pattern is similar to the period when the fishes are associated with floating objects, and the patterns according to Haedrich (1967) serve as protective coloration beneath the shifting shadows of objects, especially jellyfishes. *Nomeus* which retains its association with floating objects longer than most or all other stromateoids also retains its mottled color pattern in the largest specimens known.

Maneuverability and avoidance by the fish appear to be of primary importance in all or most stromateoid-coelenterate associations (Mansueti 1963; Horn 1970a). *Peprilus triacanthus* placed in tanks with a medusa, *Chrysaora quinquecirrha*, gradually increased the amount of time spent near the jellyfish and after 72 h remained within a 4-cm distance of the bell at least 75% of the time (Horn unpubl. data). Hovering and rapid turning were significant parts of the locomotor behavior of the fish in avoiding the tentacles of the medusa. Contact of the skin of the fish by the tentacles resulted in nematocyst firing as evidenced by the clinging of the tentacles to the fish's body causing the fish to rapidly swim away. In a two-way feeding relationship, *P. triacanthus* frequently nibbled at the manubrium and tentacles of the medusa, while weakened or otherwise slow-moving fish were captured and ingested by the medusa.

Although Lane (1960) reported that *Nomeus* can survive doses of *Physalia* toxin as much as 10 times the amount that would kill other fishes of the same size and type, *Nomeus* is stung if forced into contact with the tentacles (Lane 1960) and can be killed if touched by the tentacles according to Zahl (1952). Maul (1964) found that *Schedophilus* (= *Mupus*) *ovalis* also suffered large weals on the body from nematocysts when in contact with *Physalia* and that safety for the fish must be due in part to its ability to avoid contact with the tentacles. Mansueti (1963) concluded that in all fish-jellyfish associations the former skillfully maneuver between tentacles and generally avoid being stung but that contacts are inevitable.

Locomotion and buoyancy

The differences in locomotor behavior found between juvenile and adult stromateoids that have been observed illustrate the importance of maneuverability for juveniles and correspond to swim-bladder loss and increased independence of floating objects as maturity is reached. The paired fins are important locomotor devices among stromateoids. The pectoral fins are moved in a rotary manner for maintaining position in juveniles of *Peprilus triacanthus* and *Schedophilus medusophagus* when hovering beneath floating objects (pers. obs.) and sculled for effecting continuous swimming at less than maximum speeds in these species (Horn 1970b, unpubl. obs.) and in other stromateoids such as *Cubiceps gracilis* (Figure 8). I have observed adults of both *P. triacanthus* and *P. simillimus* in public aquaria and calculated that the pectorals are used at least 80-90% of the time as a main propulsive force at cruising speeds. The pelvic fins which may be absent (all stromateid species except one) or small (as in certain centrolophids) are well developed in juveniles of certain species. Pelvics are large in *Nomeus* and apparently important for increasing maneuverability and enhancing protective coloration for a fish living among the tentacles of *Physalia*.

The relative length of the paired fins changes with age and varies among the species (Haedrich 1967; Horn 1970b). Extremes are represented by *P. triacanthus* and *S. medusophagus* (Figures 9, 10). In *P. triacanthus* (which lacks pelvic fins) the relative length of the pectoral fin increases rapidly until the fish reaches about 75-80 mm SL beyond which the fin length ceases to increase (Figure 9). This fish size is in the range of that when the swim bladder regresses and the fish deserts its coelenterate host (Table 4). Individuals of *P. triacanthus* greater than 75-80 mm SL are negatively buoyant (see below) and swim continuously using mainly the long pectorals which also generate dynamic lift. In *S. medusophagus* the relative length of the paired fins decreases with age (Figure 10), a pattern opposite that of *P. triacanthus*. The swim bladder regresses in a size range of about 40-60 mm SL corresponding closely to the size interval during which the marked change in paired fin length occurs and apparently during which the fish deserts its coelenterate host

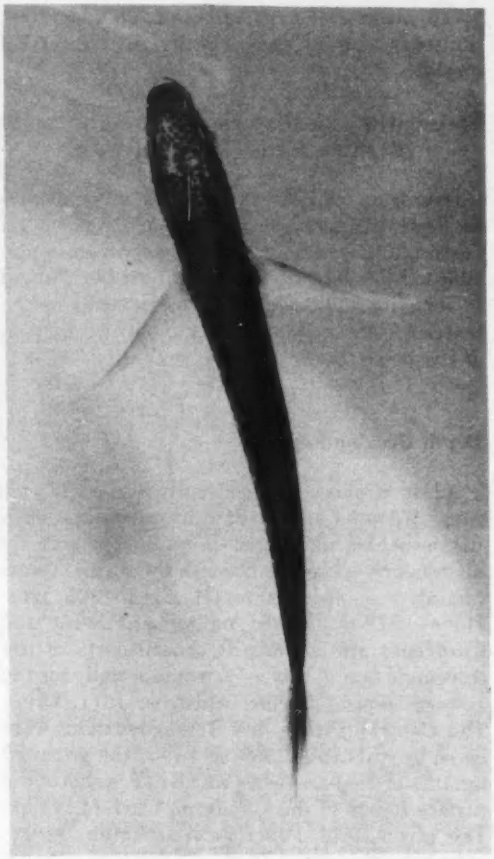

FIGURE 8.—*Cubiceps gracilis*, 68 mm SL, swimming in plastic container and using pectoral fins as principal locomotor force. Swim bladder of this fish partially regressed (see Table 4). Specimen captured at the surface in the North Atlantic.

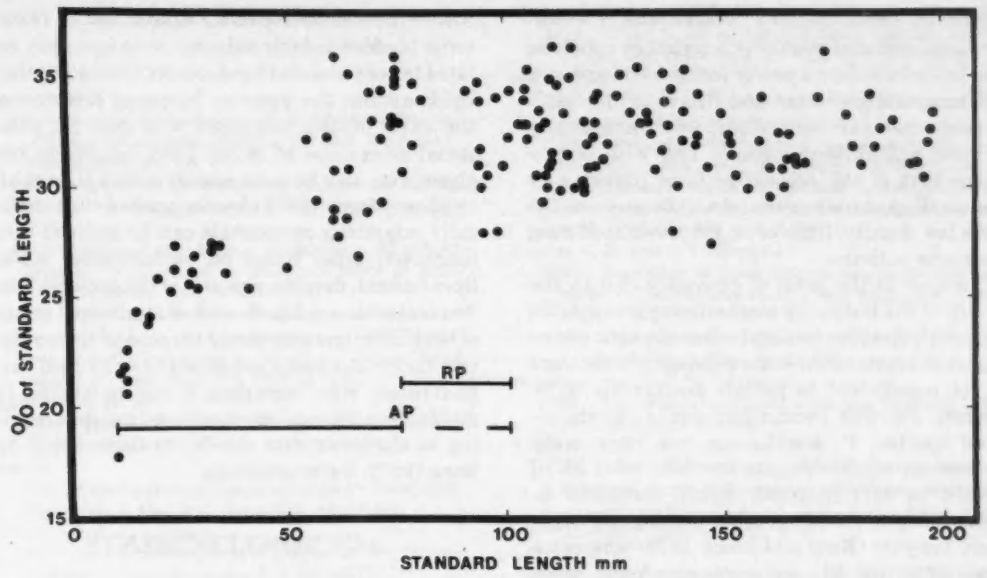

FIGURE 9.—Scatter diagram of pectoral fin length as a percentage of standard length in *Peprilus triacanthus*. RP, regression period, or size interval during which swim bladder regresses; AP, association period, or size interval during which fish associates with floating objects (dashed part of line indicates less frequent association) (see Table 4).

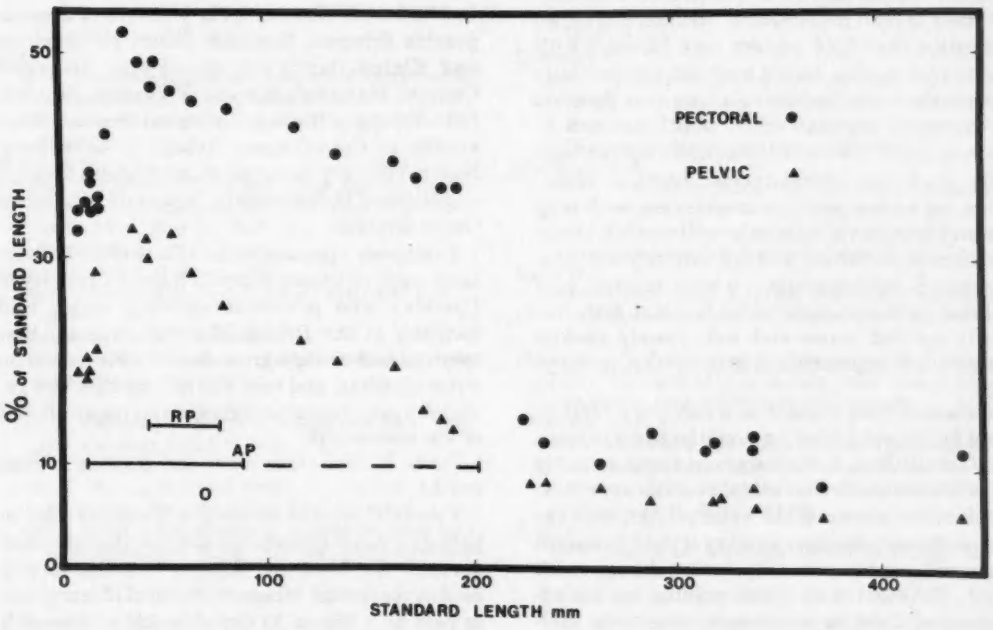

FIGURE 10.—Scatter diagram of pectoral fin and pelvic fin lengths as a percentage of standard length in *Schedophilus medusophagus*. RP and AP as in Figure 9.

(Mansueti 1963). Unlike *P. triacanthus*, *S. medusophagus* becomes neutrally buoyant or nearly so (see below) and has a poorly ossified skeleton and soft musculature (Bone and Brook 1973). Adult *S. medusophagus* swim slowly and continuously in near anguilliform manner and with only a minor part of the propulsive force provided by the small pectorals (pers. obs.). Because of the fish's low density, little or no lift is required from locomotor activity.

Changes in the level of buoyancy and in the nature of the buoyancy mechanism may coincide with swim-bladder loss and other changes occurring as stromateoids mature although the data are as yet insufficient to permit conclusions to be reached. *Peprilus triacanthus* and a closely related species, *P. simillimus*, are negatively buoyant as adults (weight in water 1.4-2.3% of weight in air) (unpubl. data). Juvenile *S. medusophagus* (85-200 mm SL) are slightly negatively buoyant (Bone and Brook 1973) whereas a larger (285 mm SL) specimen was found to be neutrally buoyant in surface seawater (unpubl. data). Large amounts of lipid have been found in adults of both *P. simillimus* and *S. medusophagus* especially in the skull and spine (Lee et al. in press). Bone and Brook (1973) found relatively low amounts of lipid in juvenile *S. medusophagus*, an indication that lipid content may increase with size in this species. Lipids may serve to partially replace the swim bladder in a buoyancy function as the organ regresses in *P. simillimus* and *S. medusophagus*, two morphologically and ecologically dissimilar stromateoids. *Peprilus simillimus*, an active, continuous swimmer with long pectoral fins, has a relatively well ossified skeleton, firm musculature, and is negatively buoyant, whereas *S. medusophagus*, a slow moving, continuous swimmer with short pectoral fins, has poorly ossified bones and soft, loosely packed muscles, and approaches or attains neutral buoyancy.

Increased lipid content as a buoyancy replacement for the swim bladder would be advantageous for *P. simillimus*, *S. medusophagus*, and probably other stromateoids that range over the upper several hundred meters of the water column since the low coefficient of compressibility of lipid compared to gas reduces the stress of pressure changes with depth. Nevenzel et al. (1969) pointed out the advantage of lipid for a vertically migrating midwater fish, and Butler and Pearcy (1972) discovered that in two such species, the myctophids *Stenobrachius leucopsarus* and *Diaphus theta*, swim bladder-to-body volumes were inversely related to body size and lipid content indicating that lipids assume the primary buoyancy function as the swim bladder regresses with age. An additional advantage of stored lipid, especially triglycerides, may be as an energy source (Lee et al. in press). Bone (1973) has suggested that vertically migrating myctophids can be grouped into functional types based on swim-bladder state, lipid content, density, and size of the pectoral fins. Stromateoids are not classed as a principal group of vertical migrators partly because of their relative rarity, but many species do have a broad vertical range. With more data, it may be possible to divide stromateoids into functional groups according to characteristics similar to those listed by Bone (1973) for myctophids.

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DISTRIBUTION AND RELATIVE ABUNDANCE OF SEVEN SPECIES OF SKATES (PISCES: RAJIDAE) WHICH OCCUR BETWEEN NOVA SCOTIA AND CAPE HATTERAS[1]

JOHN D. McEACHRAN[2] AND J. A. MUSICK[3]

ABSTRACT

Data collected during eight groundfish surveys of the area from Nova Scotia to Cape Hatteras, North Carolina, and during five seasonal surveys of Chesapeake Bight were used to define the distribution and relative abundance of *Raja eglanteria, R. garmani, R. laevis, R. erinacea, R. ocellata, R. senta,* and *R. radiata.* Ancillary distributional data for the area from the Straits of Florida to Cape Hatteras and the areas off northern Nova Scotia and the Gulf of St. Lawrence were used qualitatively to extend the distributional study.

Raja eglanteria is a Carolinian species abundant north of Cape Hatteras only during the warmer months. *Raja garmani,* a skate of the outer continental shelf and upper slope, consists of two populations which have different temperature preferences. *Raja laevis* is the most widespread species studied and does not appear to be as abundant as the other skates in any region of the study. *Raja erinacea,* a Virginian to boreal species, occurs from southern Nova Scotia to Cape Hatteras in shallow water but is present at depths down to 384 m. *Raja ocellata* is a Virginian to boreal species distributed similarly to *R. erinacea* except that the former is widespread in the Gulf of St. Lawrence and off northern Nova Scotia. *Raja senta,* a boreal species, frequently occurs on the northern offshore banks of Nova Scotia and at temperatures as low as −1.3°C. *Raja radiata* is a boreal to arctic species.

Raja erinacea and *R. ocellata* are sympatric over the greater part of their ranges as are *R. senta* and *R. radiata.* The two pairs of species have complementary distributions. *Raja ocellata* has slightly lower temperature preferences than *R. erinacea,* and *R. radiata* is more widespread and has wider temperature tolerances than *R. senta.*

The genus *Raja* is represented by *R. eglanteria, R. garmani, R. laevis, R. erinacea, R. ocellata, R. senta* and *R. radiata* along the continental shelf of North America between Nova Scotia and Cape Hatteras, NC. Notes on the occurrence and distribution of these species have been summarized by Bigelow and Schroeder (1953, 1954), Leim and Scott (1966), and McEachran (1973); however, most of this information is based on scattered regional studies. The present study presents data gathered during comprehensive groundfish surveys of the area from Nova Scotia to Cape Hatteras and defines the distribution and relative abundance of each species, as well as cooccurrence among species.

MATERIALS AND METHODS

Data used in this study were divided into two categories: 1) quantitative data used to determine relative abundance of the skates, and 2) qualitative data used only to determine the temperature, depth, and geographical ranges of the skates.

Data supplied by National Marine Fisheries Service (NMFS) Biological Laboratory at Woods Hole, Mass. (now Northeast Fisheries Center) and by the Virginia Institute of Marine Science (VIMS) at Gloucester Point, Va. were used to determine relative abundance. The former data consisted of eight groundfish surveys of the continental shelf (27-366 m) from LaHave Bank, off southeastern Nova Scotia, and the Gulf of Maine to Cape Hatteras. A total of 2,247 stations were made during the winters of 1968-70, the summer of 1969, and the autumns of 1967-70 (Table 1) by the RV *Albatross IV,* except that part of 70-06 was conducted by the RV *Delaware II.* The survey area was divided into 58 strata according to depth and geographical area, and three or more stations were randomly selected within each stratum per cruise (Figure 1) (Grosslein 1969). A No. 36 Yankee trawl equipped with a cod end liner of 0.25-inch bar mesh and

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TABLE 1.—Groundfish surveys conducted by the Biological Laboratory of the National Marine Fisheries Service at Woods Hole, Mass (now Northeast Fisheries Center).

Cruise	Dates	Season	No. of stations
67-21	17 Oct.- 9 Dec. 1967	Autumn	271
68-03	4 Mar.- 16 May 1968	Winter	262
68-17	10 Oct.- 26 Nov. 1968	Autumn	275
69-02	5 Mar.- 10 Apr. 1969	Winter	266
69-06	14 July- 18 Aug. 1969	Summer	267
69-11	8 Oct.- 23 Nov. 1969	Autumn	276
70-03	12 Mar.- 29 Apr. 1970	Winter	289
70-01	15 Oct.- 20 Nov. 1970	Autumn	341
Total			2,247

18 inch rollers on the ground rope was towed at 3.5 knots for 0.5 h at each station. Distance of tow averaged 1.75 miles.

Prior to data analysis, the 58 sampling strata were grouped into five ecological subareas according to hydrography and substratum. Schopf and Colton (1966) stated that the southern Nova Scotian shelf, Gulf of Maine, and Georges Bank have different bottom temperatures and faunal assemblages. Although Georges Bank and Nantucket shoals (northern section of the mid-Atlantic Bight) have similar bottom temperatures and faunal assemblages (Schopf and Colton 1966), the area extending from Georges Bank to Cape Hatteras was subdivided because of its great size. The southern section of the mid-Atlantic Bight consisted of strata 61 to 76; the northern mid-Atlantic Bight was composed of strata 1 to 12 and 25; Georges Bank was made up of strata 13 to 23; the Gulf of Maine included strata 24, 26 to 30, and 36 to 40; and the Nova Scotian shelf consisted of strata 31 to 35, 41, and 42. All four depth zones (27-55, 56-110, 111-183, 184-366 m) were sampled in the first three subareas; the three deeper zones were surveyed in the Gulf of Maine; and only two zones, 56-110 and 111-183 m, were sampled on the Nova Scotian shelf.

Preliminary examination of the skate data indicated contagion as Taylor (1953) and Roessler (1965) had demonstrated for trawl catch data in general. A logarithmic transformation tends to normalize contagious distributions (Pereyra et al. 1967), so skate counts were transformed to log $(X + 1)$. Transformed values were used to determine the geometric mean numbers (indices of abundance) of skates per stratum per cruise. The indices of abundance were weighted by dividing them by the area of the strata to correct

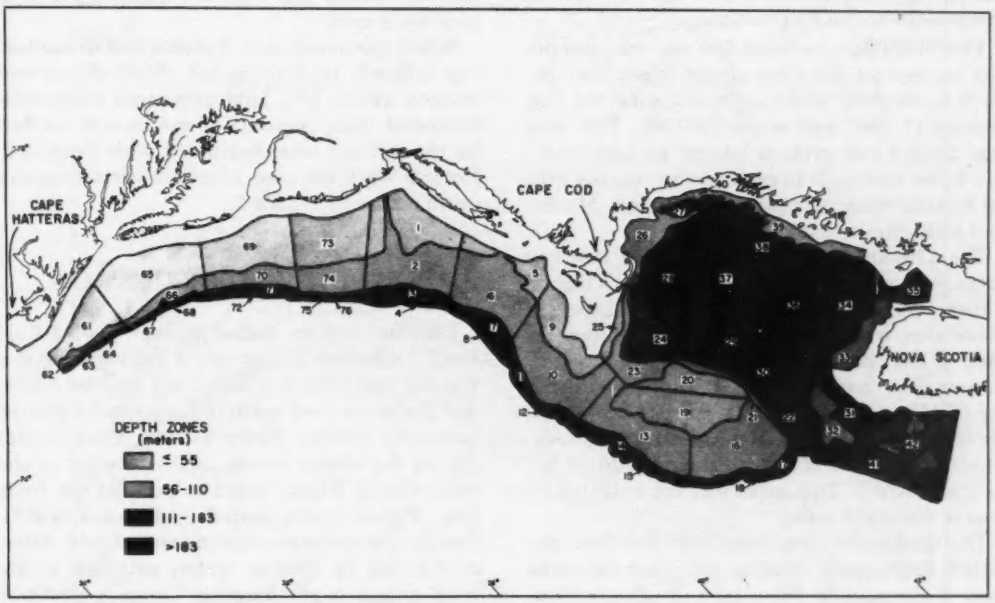

FIGURE 1.—Strata sampled by the RV *Albatross IV* and *Delaware II*, 1967-70. Strata numbers 43-60 were not included in the surveys.

for areal differences between strata. Area of the strata are listed in Table 2.

Indices of abundance for all stations, within temperature intervals of 1°C for each of the five ecological subareas, were calculated for each species. Indices were not weighted. Length frequencies were calculated for strata sets corresponding to each of the four depth intervals (27-55, 56-110, 111-183, 184-366 m) within each of the subareas. This analysis gave the percentages that each 3-cm length increment contributed to the total catch of a species within each of the strata sets of the subareas.

Hurlbert's (1969) index of association was used to determine the level of cooccurrence based on presence and absence of two species at the same stations. Species pairs with a significant positive index were compared by the product moment correlation (simple correlation coefficient) to determine if the two species were positively or negatively related by numbers. The correlation indices were computed from transformed abundance values [log $(X + 1)$] at stations where the two species cooccurred. According to Hurlbert (1969), a negative correlation, showing an inverse relationship in numbers of individuals between the species, may indicate that the two species compete for the same resources.

The VIMS data included five seasonal groundfish surveys of the Chesapeake Bight (lat. 38° 43′N to 35°13′N) in 9 to 274 m during the four seasons of 1967 and winter of 1968. This area was divided into grids of lat. 15′ by long. 12.5′. A 1-h tow was made in each grid per survey with an Atlantic western trawl without rollers (Musick and McEachran 1972).

The Chesapeake Bight was divided into two areas, one north and one south of the Virginia Capes (lat. 37°N) for data analysis. Index of abundance (geometric mean) was computed for each of the species (*R. eglanteria, R. garmani, R. erinacea,* and *R. ocellata*) captured during the VIMS survey, by depth zone (0-18, 19-37, 38-73, 74-110, 111-165, 166-274 m) and by temperature intervals of 1°C, north and south of lat. 37°N separately. This index was not weighted by area of the depth zone.

The qualitative data were obtained from the NMFS Exploratory Fishing and Gear Research Base at Pascagoula, Miss. (now Southeast Fisheries Center, Pascagoula Laboratory) for the area from the Straits of Florida to Cape Hatteras, and from the Fisheries Research Board of Canada Biological Station at St. Andrews, New Brunswick for the area off northeastern Nova Scotia, including Banquereau, Sable Island Bank, Western Bank, and the Gulf of St. Lawrence. Distributional data from south of Cape Hatteras were collected from 1961 to 1968, and data from northeastern Nova Scotia and the Gulf of St. Lawrence were collected from 1960 to 1970. Several vessels and different types of trawling gear were used.

TABLE 2.—Area of sampling strata.

Stratum number	Area (mi²)	Stratum number	Area (mi²)	Stratum number	Area (mi²)
1	2,516	21	424	40	578
2	2,078	22	454	41	3,752
3	566	23	1,016	42	589
4	188	24	2,569	61	1,318
5	1,475	25	390	62	243
6	2,554	26	1,014	63	86
7	514	27	720	64	60
8	230	28	2,249	65	2,832
9	1,522	29	3,245	66	555
10	2,722	30	619	67	86
11	622	31	2,185	68	52
12	176	32	712	69	2,433
13	2,374	33	816	70	1,024
14	656	34	1,766	71	281
15	230	35	1,097	72	105
16	2,980	36	4,069	73	2,145
17	360	37	2,108	74	1,273
18	172	38	2,560	75	139
19	2,454	39	730	76	60
20	1,221				

Small specimens of *R. erinacea* and *R. ocellata* are difficult to distinguish (McEachran and Musick 1973), and field personnel often misidentified them. Records of species not verified by the authors were evaluated with discretion. Records were not used when the correct species could not be determined.

RESULTS AND DISCUSSION

Seasonal bottom isotherms were plotted from the RV *Albatross IV* surveys of 1969 because this was the only year that included a summer cruise, and the winter and autumn temperature profiles appeared typical. Temperatures were lowest during the winter survey, and isotherms in the mid-Atlantic Bight tended to parallel the coast line (Figure 2), as stated by Bigelow (1933). During the summer cruise a mass of cold water, surrounded by warmer water, extended southward almost to the Virginia Capes, a condition previously described by Bigelow (1933). Temperatures were warmest during the autumn survey.

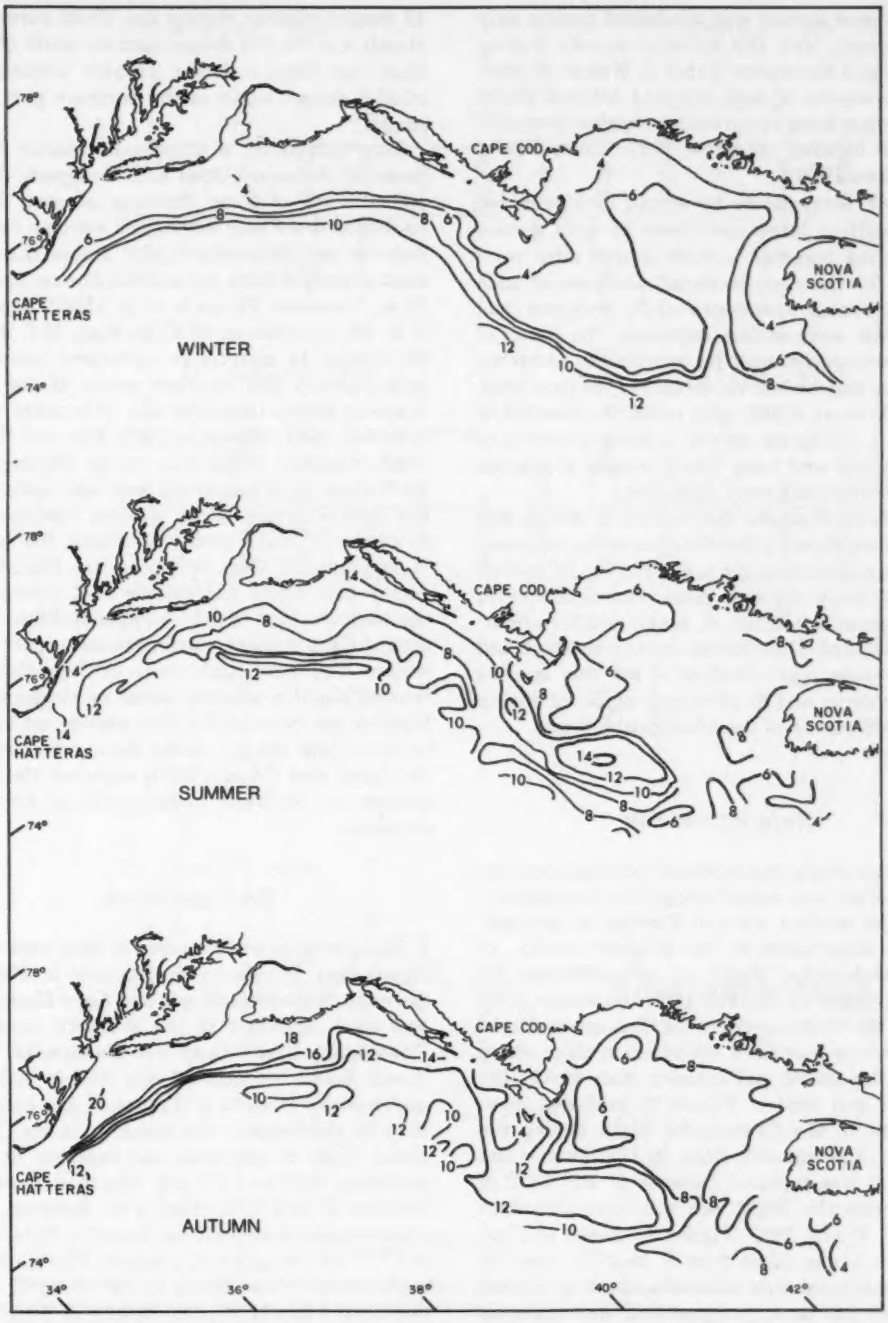

FIGURE 2.—Bottom isotherms plotted from measurements taken during winter, summer, and autumn 1969 surveys of the RV *Albatross IV*. Temperatures are in degrees Celsius.

The summer survey was conducted during July and August, and the autumn survey during October and November (Table 1). Waters of intermediate depths of both the mid-Atlantic Bight and Georges Bank reach their maximum temperatures in October (Bigelow 1927, 1933; Schopf and Colton 1966).

Length frequencies by strata sets revealed that small to large specimens of each species were found together and all length sizes were pooled for the distributional analyses of each species. Small specimens of *R. erinacea* and *R. ocellata* were seldom captured. The young of these two species may lie outside the sampling region or may be less vulnerable to the gear used. Richards et al. (1963) also noted the absence of young *R. erinacea* on the fishing grounds of Block Island and Long Island sounds where the larger individuals were abundant.

Charts showing the distribution by strata, and histograms showing the distribution by temperature were illustrated for the *Albatross IV* cruises of 1969. Only the four most abundant species (*R. erinacea, R. ocellata, R. senta,* and *R. radiata*) were included. Distribution by temperature and depth zones was illustrated for two species (*R. eglanteria* and *R. garmani*) captured during the VIMS survey of the Chesapeake Bight.

Raja eglanteria

Raja eglanteria was captured from the southern section of the mid-Atlantic Bight to about midway along the eastern coast of Florida. A few individuals were taken in the southern section of the mid-Atlantic Bight on all *Albatross IV* cruises, except for summer 1969 and winter 1970. During the VIMS survey of the Chesapeake Bight *R. eglanteria* was more abundant in shoal water during the spring and summer than during the autumn and winter (Figure 3) and was more abundant in the Chesapeake Bight during the summer and autumn than in the winter and spring. It was captured between 5° and 26°C in the Chesapeake Bight and was most abundant between 9° and 20°C (Figure 4). South of Cape Hatteras it was taken from 9° to 27°C. Over its entire range, it was most abundant at depths less than 111 m. *Raja eglanteria* was captured only at 9 of the 676 stations which were in water deeper than 110 m. It was taken at 5 of the 43 deeper stations during the VIMS survey but at only 4 of the 633 deeper stations south of Cape Hatteras, thus it has a greater tendency to inhabit deeper water in the northern part of its range.

Raja eglanteria, a Carolinian species in the sense of Johnson (1934) and Hedgpeth (1957), occurs north of Cape Hatteras all year but is abundant there only during the warmer months. Bigelow and Schroeder (1953) stated that it is most abundant from the sublitoral zone to about 55 m. However, Edwards et al. (1962) captured it in 280 and 329 m off Cape May, N.J. during the winter. In autumn, *R. eglanteria* leaves the embayments and shallow areas of the mid-Atlantic Bight (Bigelow and Schroeder 1953; Schwartz 1961; Massman 1962; Fitz and Daiber 1963; Schaefer 1967) and moves offshore and southward. *Raja eglanteria* was not captured in the mid-Atlantic Bight during the summer *Albatross IV* cruise probably because the species is concentrated then at depths less than 27 m. Apparently many individuals that summer in the southern part of the Chesapeake Bight move around Cape Hatteras during the autumn or early winter. The individuals south of Cape Hatteras inhabit slightly warmer water as suggested by Bigelow and Schroeder (1953) and do not appear to move into deeper water during the winter. Dahlberg and Odum (1970) reported that this species is resident year-round in Georgia estuaries.

Raja garmani

Raja garmani was captured in deep water from Nantucket Shoals to the Straits of Florida. Between Nantucket Shoals and Cape Hatteras it was most abundant in the southern section of Chesapeake Bight. Over the Chesapeake Bight it was found between 33 and 196 m and generally deeper than 73 m (Figure 5), and appeared to move shoreward in the summer. In the Chesapeake Bight *R. garmani* was captured at temperatures of 6° to 17°C and was most abundant bewteen 9° and 13°C (Figure 6). Between Cape Hatteras and Georgia it was found in 66 to 123 m at 17°C; off Georgia and northern Florida it was captured in 77 to 155 m at 11° to 19°C. From northern Florida to the Straits of Florida it occurred in 99 to 366 m at 17°C, and all but one of the captures were in 183 to 366 m.

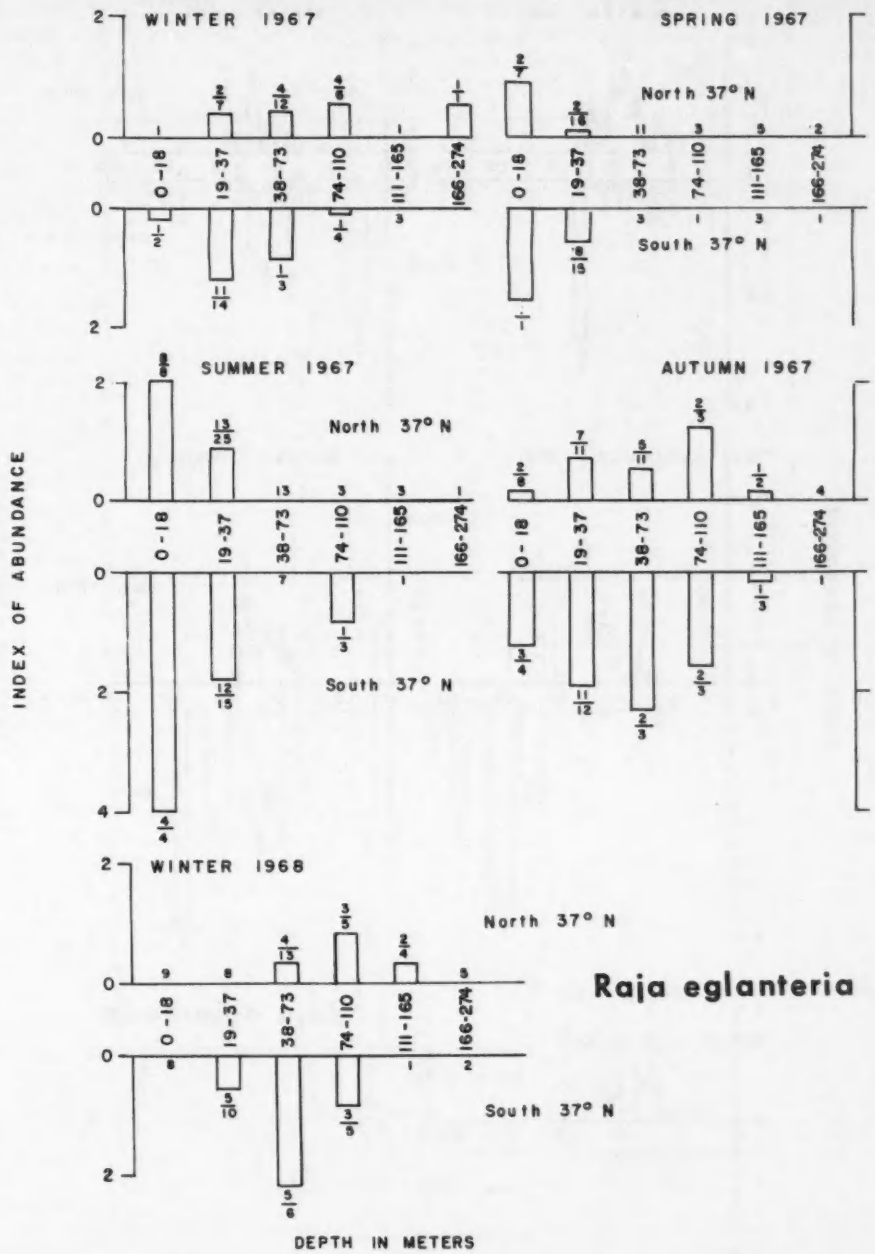

FIGURE 3.—Index of abundance (geometric mean) of *Raja eglanteria* captured in Chesapeake Bight during each cruise within each depth stratum. Data collected north and south of lat. 37°N were analyzed separately. The fraction over each bar is the ratio of the number of stations at which the species was captured to the total number of stations in each stratum. Whole numbers represent the number of stations in the strata in which no specimens were captured.

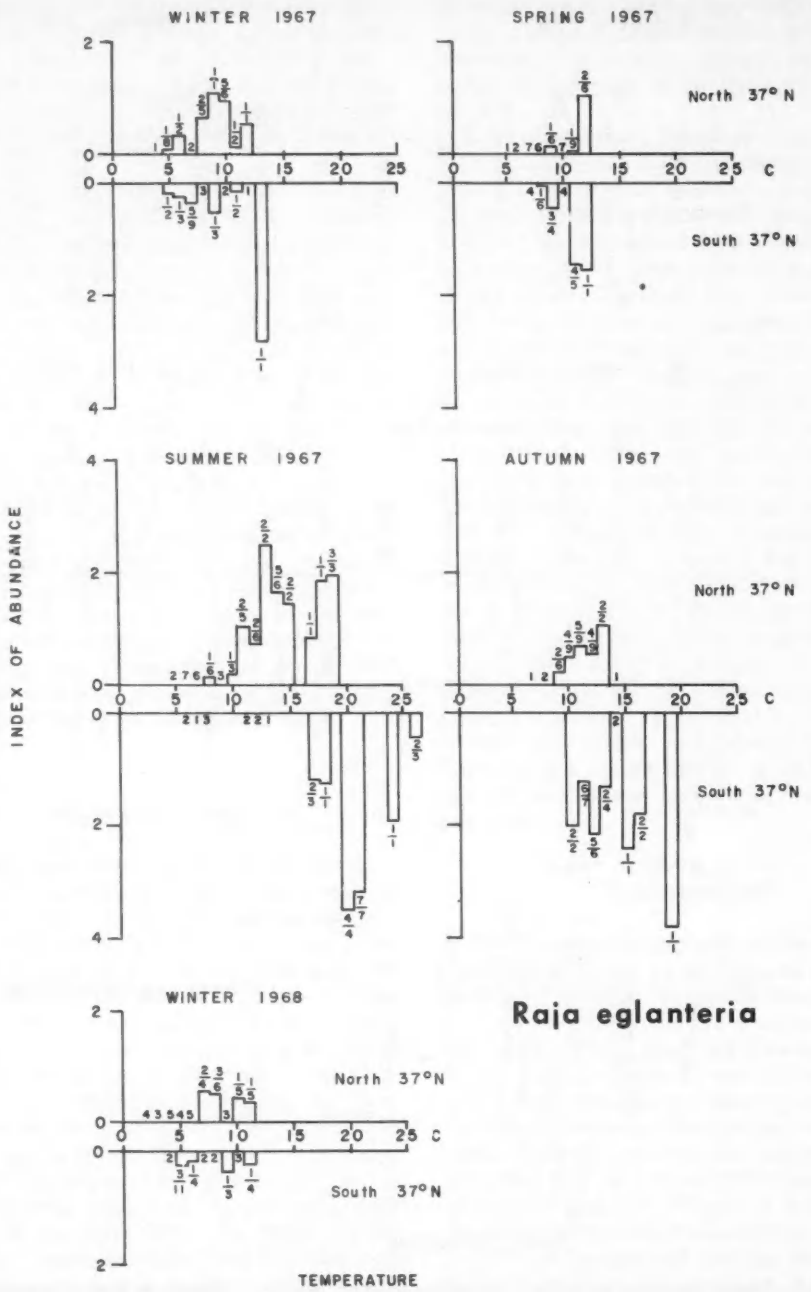

FIGURE 4.—Index of abundance (geometric mean) of *Raja eglanteria* captured in the Chesapeake Bight during each cruise within temperature intervals of 1°C. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for explanation of fractions and whole numbers.

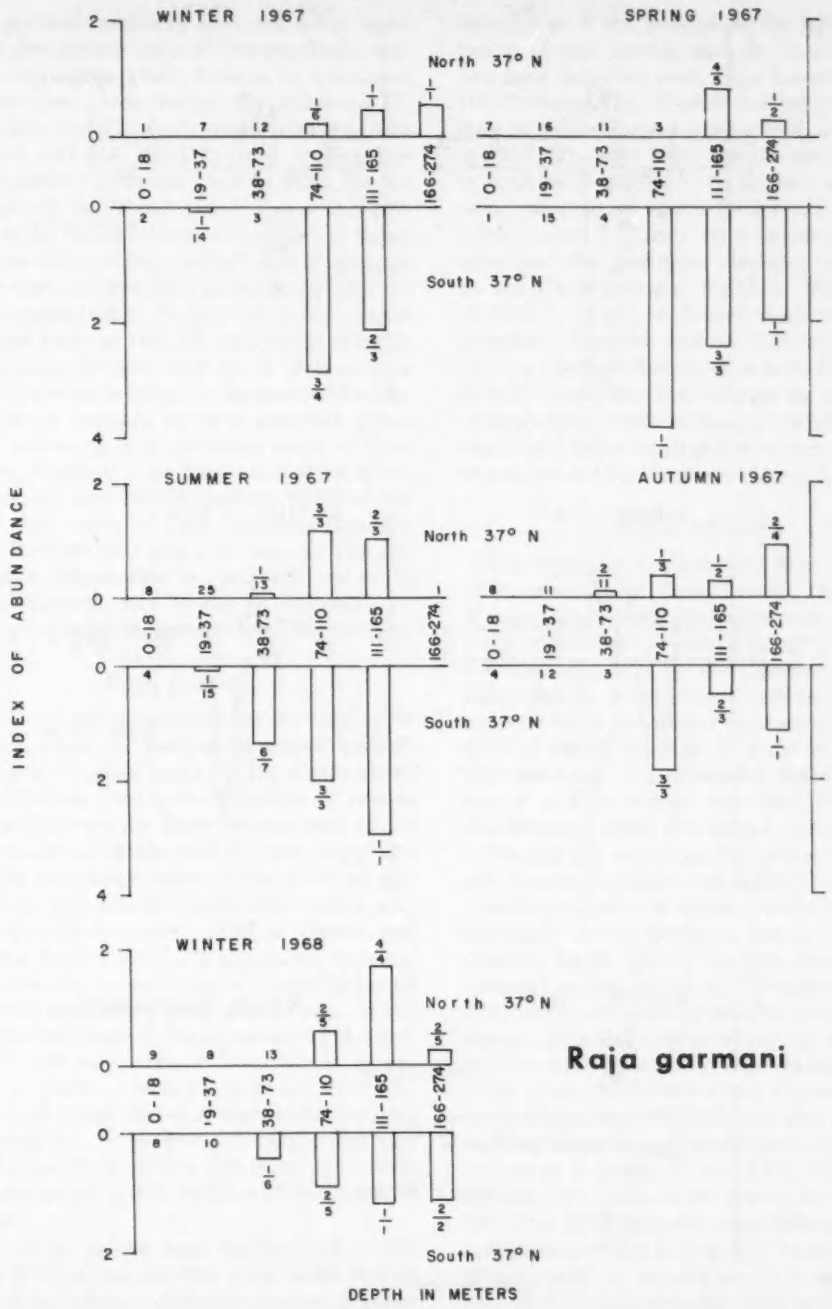

FIGURE 5.—Index of abundance (geometric mean) of *Raja garmani* captured in the Chesapeake Bight during each cruise within each depth stratum. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for an explanation of fractions and whole numbers.

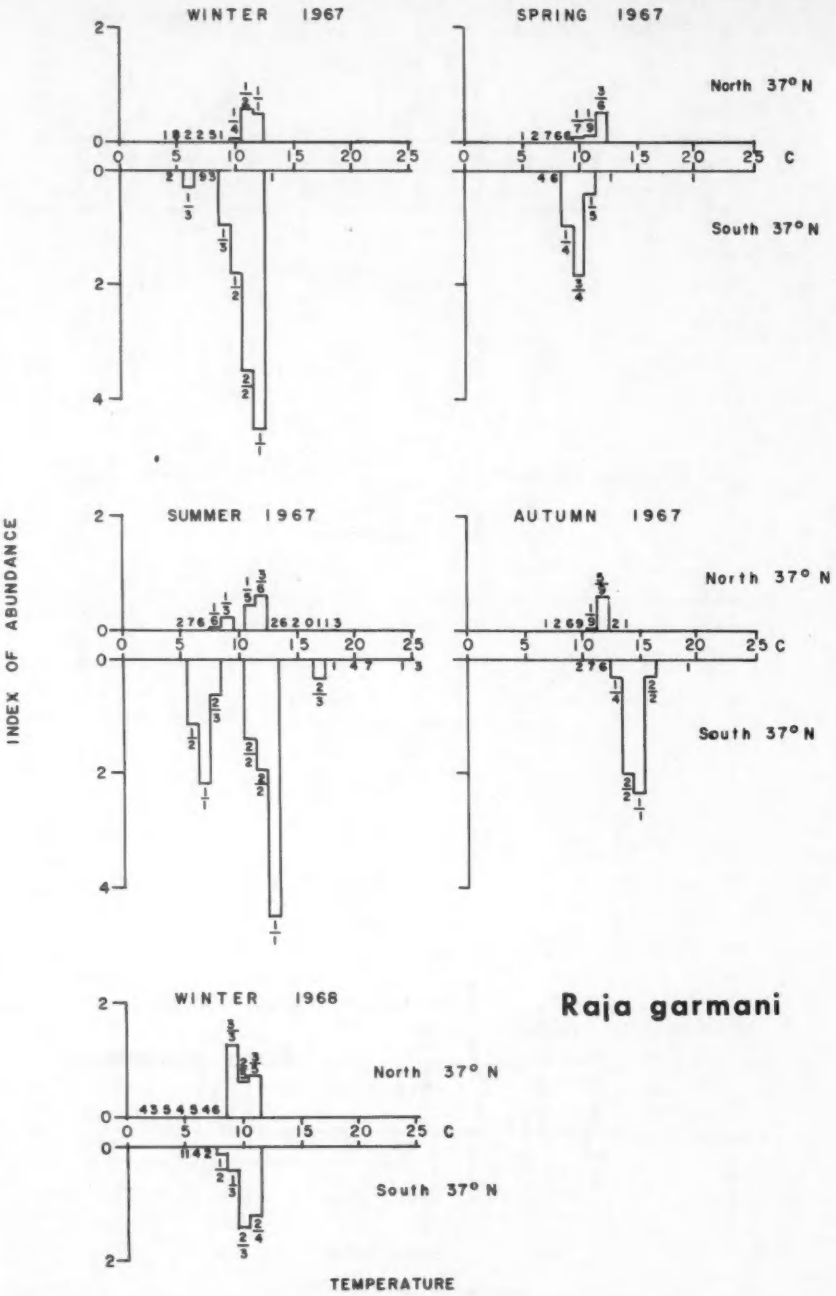

FIGURE 6.—Index of abundance (geometric mean) of *Raja garmani* captured in the Chesapeake Bight during each cruise within temperature intervals of 1°C. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for explanation of fractions and whole numbers.

Raja garmani probably does not occur regularly on the eastern slope of Georges Bank, contrary to Schroeder (1955), because no specimens were captured there during the *Albatross IV* cruises. The depth and temperature ranges of 51 to 494 m and 5.3° to 15°C given by Bigelow and Schroeder (1953) are close to those for the area north of Cape Hatteras in the present study. It has more limited depth range and is found in warmer water in the southern part of its range than in the northern part as stated by Bigelow and Schroeder (1953). Staiger (1970) stated that it is found between the 119- and 366-m isobaths on Pourtales Terrace, and north of Pourtales Terrace it occurs in 183 m up the coast of Florida. This species appears to have separate populations, one north and the other south of Cape Hatteras. North of Cape Hatteras mature specimens are 335 mm TL (McEachran 1970) to 439 mm TL and south of Cape Hatteras they are mature between 250 and 314 mm TL. The differences in temperature ranges north and south of Cape Hatteras may be due to differences in physiological requirements of the two populations.

Raja laevis

Raja laevis was captured from the Gulf of St. Lawrence, along the northeastern coast and offshore banks of Nova Scotia, to the northeastern coast of Florida. During the *Albatross IV* cruises it was taken from the Nova Scotian shelf to the southern section of the mid-Atlantic Bight and was most frequently taken in the northern section of the mid-Atlantic Bight, the eastern part of Georges Bank, eastern Gulf of Maine, and the Nova Scotian shelf. No specimens were obtained from the western Gulf of Maine. Seasonal changes in abundance were not evident. In the Gulf of St. Lawrence, *R. laevis* was found in 315 m at 4.7°C. Off northeastern Nova Scotia it was caught at depths of 24 to 375 m at 1.2° to 10.7°C. Depths and temperatures at capture for the area from southern Nova Scotia to Cape Hatteras ranged from 38 to 351 m and 3° to 20°C. *Raja laevis* was caught in 302 to 368 m off northeastern Florida.

Raja laevis is the most widespread of the species studied, but too few were taken during this study to elaborate on its distribution. Bigelow and Schroeder (1953) stated that this species occurs from the tidemark to about 750 m at 1.2° to 20°C. The southern limit of its range remains in doubt because of the apparent confusion of this species with *R. floridana* which has been captured from Cape Lookout, N.C. to Dry Tortugas, Fla. (Bigelow and Schroeder 1968). *Raja floridana* is very similar to *R. laevis* (Bigelow and Schroeder 1962) and the specimens used to describe *R. floridana* came from some of the same stations at which Bullis and Thompson (1965) listed *R. laevis*. The senior author has examined the specimens identified as *R. laevis* at the United States National Museum and University of Miami School of Marine and Atmospheric Sciences, and all of those from south of Cape Hatteras have proven to be *R. floridana*. Also *R. laevis* does not occur in the species lists of Struhsaker (1969) or Staiger (1970). Thus it is likely that many or all of the records of *R. laevis* from south of Cape Hatteras refer to *R. floridana*.

Raja erinacea

Raja erinacea was recorded from the Gulf of St. Lawrence; off Cape Breton, Nova Scotia; Western Bank; and two specimens were positively identified from Sable Island Bank. It was the most abundant species captured on Georges Bank and in the northern section of the mid-Atlantic Bight. It was rarely taken in the western Gulf of Maine (Figure 7). *Raja erinacea* was most abundant in Chesapeake Bight during the winter and those that remained there during the summer moved into deeper water.

Throughout its range, *R. erinacea* was generally caught at depths less than 111 m, but was occasionally taken at depths greater than 183 m, especially in the northern section of the mid-Atlantic Bight and on Georges Bank where it occurred as deep as 329 m. Edwards et al. (1962) captured *R. erinacea* as deep as 384 m off New Jersey, thus the species is not as restricted to shallow water as stated by Bigelow and Schroeder (1954) who reported that 159 m was the maximum depth of the species. Temperatures at depth of capture ranged from 2° to 19°C with most captures occurring between 2° and 15°C. The recorded temperature range of the species is 1.2°C (Tyler 1971) to 21°C (Bigelow and Schroeder 1953).

Raja erinacea is a Virginian to boreal species whose center of abundance is in the northern section of the mid-Atlantic Bight and on Georges Bank. Only in these areas was it found year-round over almost the entire range of temperatures recorded for the areas (Figures 8-10). In

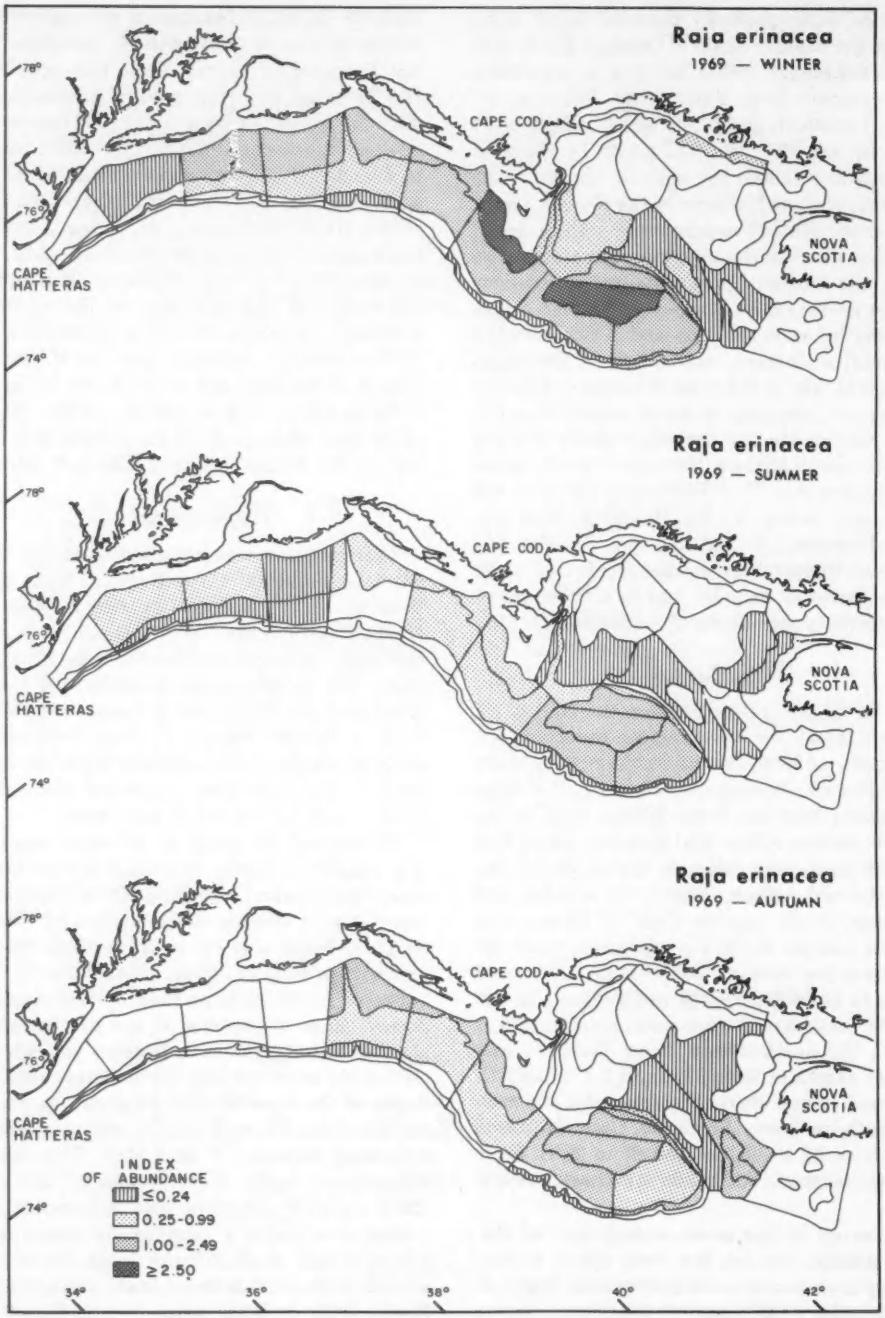

FIGURE 7.—Index of abundance (geometric mean) of *Raja erinacea* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

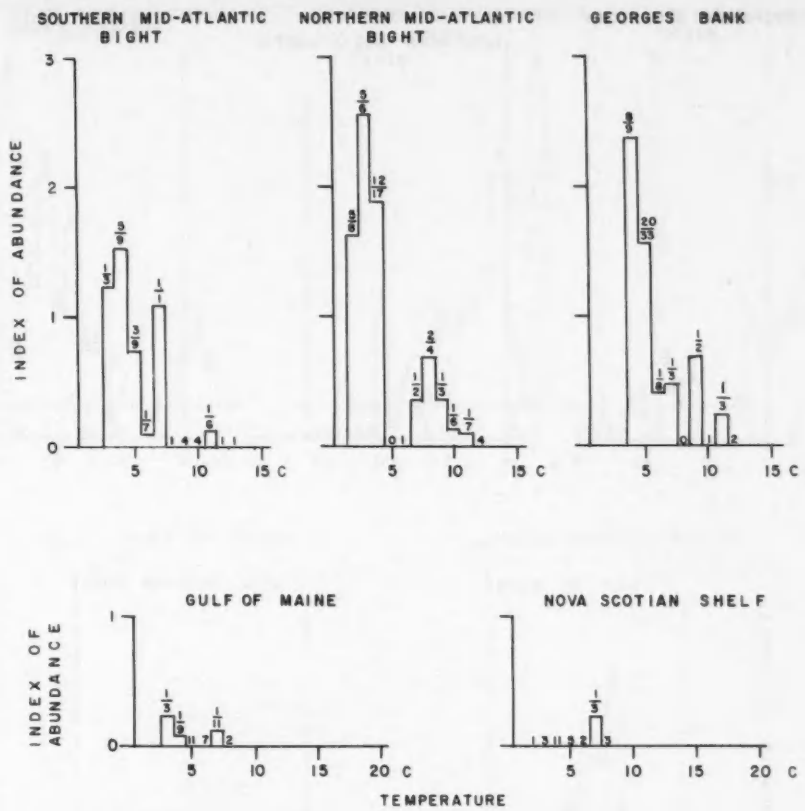

FIGURE 8.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

the southern section of the mid-Atlantic Bight it was usually caught in the lower part of the area's temperature range, and on the Nova Scotian shelf in the upper part of the temperature range.

Along the inshore fringe of its range the species moves onshore and offshore with seasonal temperature changes as stated by Bigelow and Schroeder (1953); Merriman et al. (1953); Fitz and Daiber (1963); Richards (1963); Schaefer (1967); and Tyler (1971, 1972). *Raja erinacea* also moves north and south with seasonal temperature changes along the southern fringe of its range. Contrary to Bigelow and Schroeder (1953) and Leim and Scott (1966), *R. erinacea* probably does not regularly occur off Nova Scotia north of LaHave Bank, and it may be entirely absent in the Gulf of St. Lawrence (McEachran 1973).

Raja ocellata

Raja ocellata was frequently taken in the Gulf of St. Lawrence, off northeastern Nova Scotia, and the offshore banks of Banquereau, Sable Island, and Western Bank. It was second to *R. erinacea* in abundance on Georges Bank and in the northern section of the mid-Atlantic Bight (Figure 11). *Raja ocellata* was much more abundant in the southern section of the mid-Atlantic Bight during the winter than during the remainder of the year. This species was most frequently captured in water shallower than 111 m, but was occasionally caught deeper than the maximum depth of 110 m recorded by Bigelow and Schroeder (1953). In the Gulf of Maine it was taken at 205 m, and in the Gulf of St.

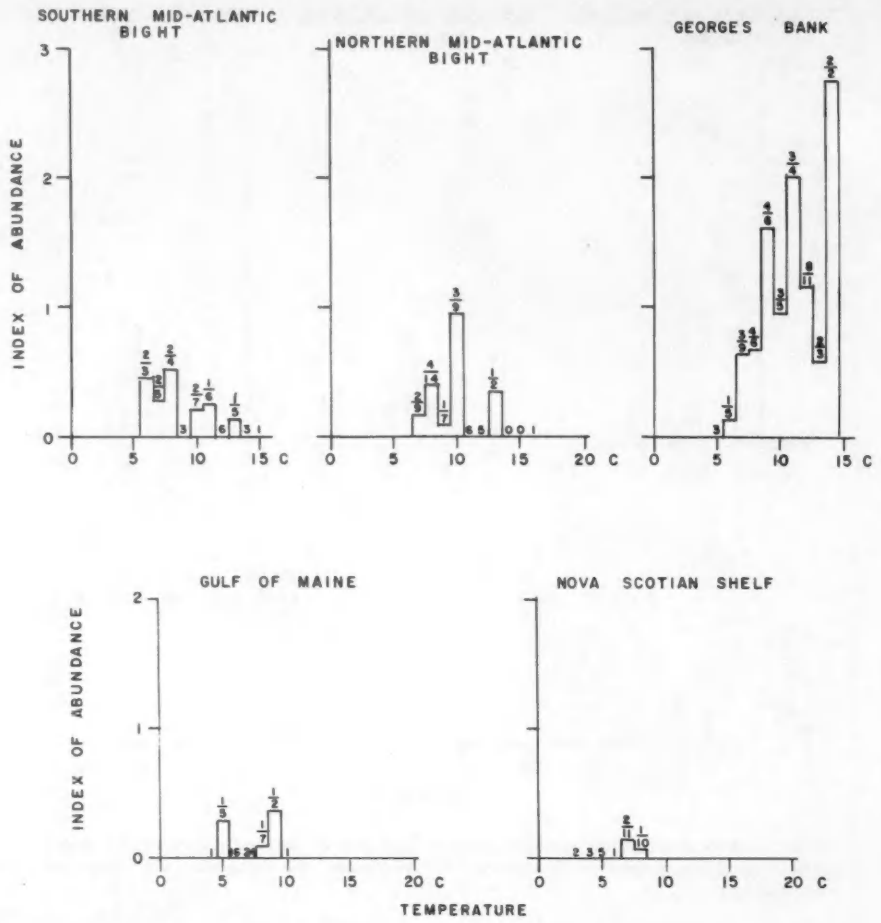

FIGURE 9.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Lawrence as deep as 371 m. Temperatures at depth of capture ranged from −1.2° to 4.8°C in the Gulf of St. Lawrence, 1.1° to 12.7°C off northeastern Nova Scotia, and 2° to 15°C from southern Nova Scotia to Cape Hatteras. Only in the Gulf of St. Lawrence was *R. ocellata* taken at temperatures below its previously recorded temperature range of 1.2°C (Tyler 1971) to 19°C (Bigelow and Schroeder 1953).

Raja ocellata is a Virginian to boreal species whose center of abundance is on Georges Bank and in the northern section of the mid-Atlantic Bight. In both subareas it was found year-round over almost the entire temperature range for the areas (Figures 12-14). It was captured only at the lower part of the temperature range recorded for the southern section of the mid-Atlantic Bight and at higher temperatures recorded for the Nova Scotian shelf.

This species was widespread in the Gulf of St. Lawrence, off northeastern Nova Scotia, and the offshore banks, and it was not as abundant as *R. erinacea* in the southern mid-Atlantic Bight. All reports of *R. erinacea* from the Gulf of St. Lawrence and most records of it from northern Nova Scotia probably refer to *R. ocellata*.

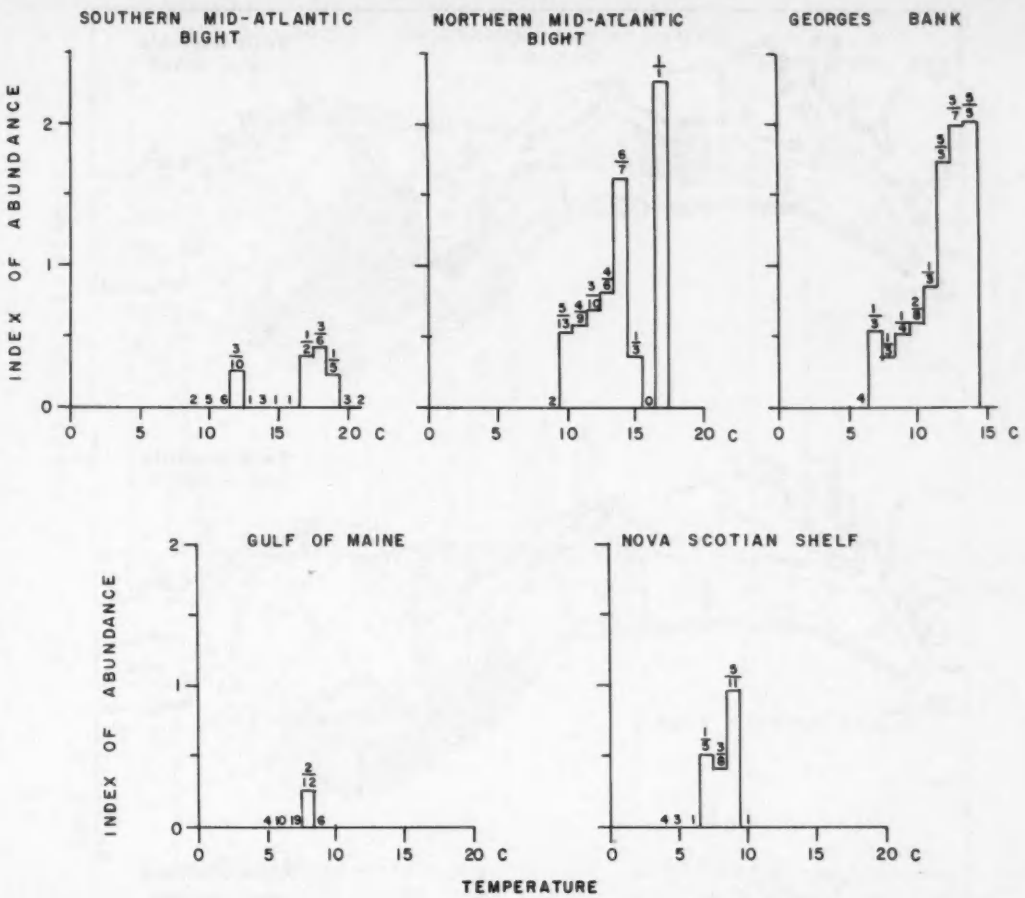

FIGURE 10.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Raja senta

Raja senta was taken in the Gulf of St. Lawrence, along the northeastern coast of Nova Scotia and, contrary to the reports of Bigelow and Schroeder (1953) and Leim and Scott (1966), it was fairly abundant on the offshore banks of Banquereau, Sable Island, and Western. It was found throughout the Gulf of Maine, off southern Nova Scotia, and on Georges Bank (Figure 15). No seasonal trends in abundance were noted. Depth of capture ranged from 31 to 413 m but it was most abundant below 110 m. Bigelow and Schroeder (1953) stated that *R. senta* occurred between 46 and 874 m and was most abundant between 91 and 457 m. This species was found at temperatures from 0.5° to 4.8°C in the Gulf of St. Lawrence, −1.3° to 11.8°C off northeastern Nova Scotia, and 2° to 10°C from southern Nova Scotia to Georges Bank. In the northern part of its range, it was occasionally caught at temperatures less than 2°C, which Bigelow and Schroeder (1953) stated was the minimum temperature for the species.

Raja senta is a boreal species whose center of abundance occurs in the Gulf of Maine, where it is found over the greater part of the range of temperatures (Figures 16-18). It is found only at the lower part of the temperature range on Georges Bank.

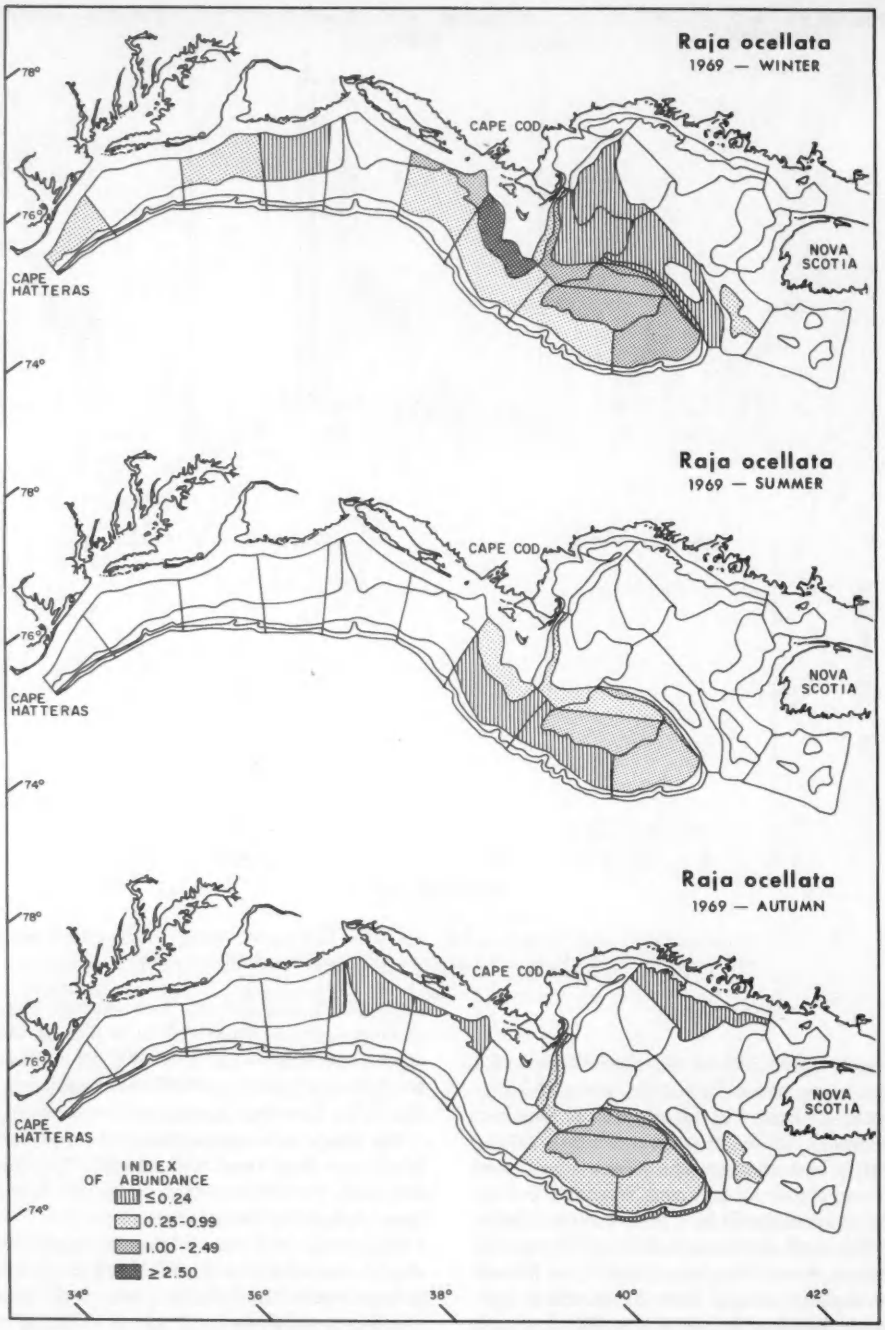

FIGURE 11.—Index of abundance (geometric mean) of *Raja ocellata* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

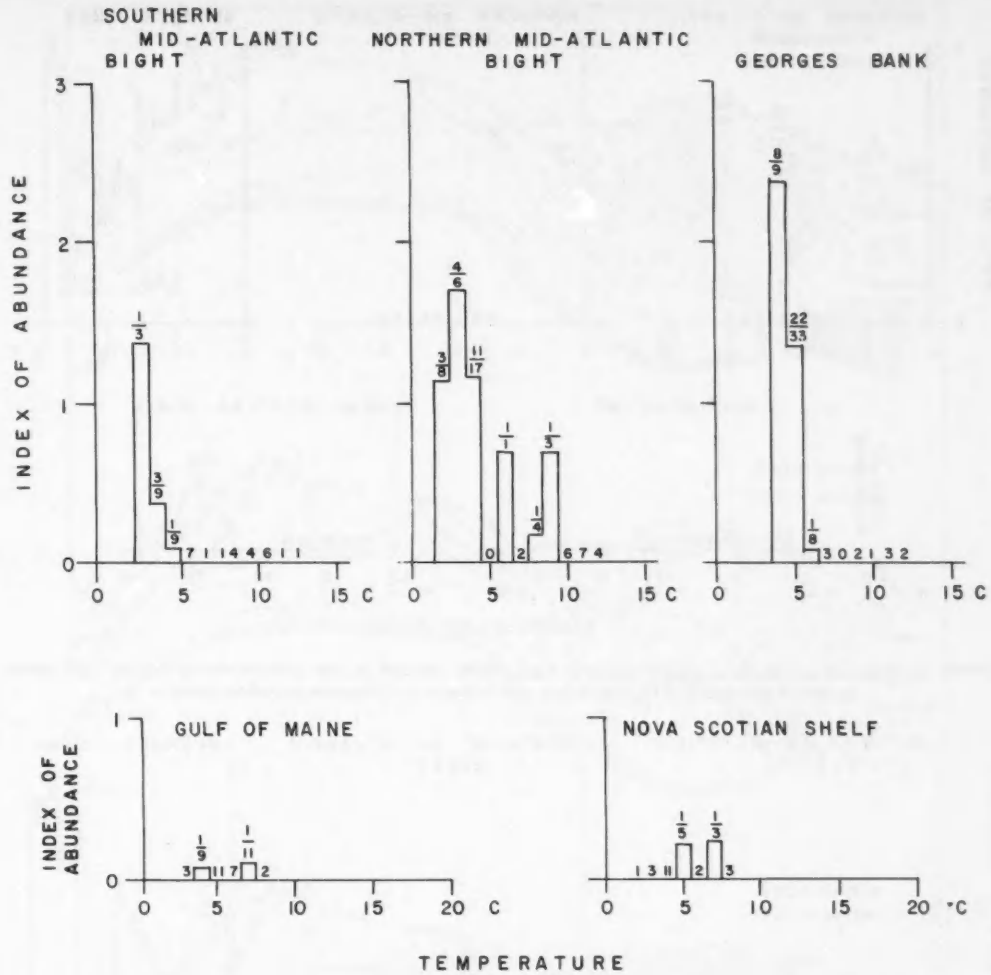

FIGURE 12.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Raja radiata

Raja radiata was the most abundant skate encountered in the Gulf of St. Lawrence, off northeastern and southeastern Nova Scotia, and in the Gulf of Maine. It was widespread along the eastern and northwestern slopes of Georges Bank (Figure 19). *Raja radiata* occurred between 27 and 439 m but was most abundant between 111 and 366 m. Bigelow and Schroeder (1953) listed a depth range of 18 to 896 m for this species in the western Atlantic. Temperatures at which it was captured ranged from −1.3° to 14°C. The previously recorded temperature range was −1.4°C (Backus, 1957) to 10°C (Bigelow and Schroeder 1953).

Raja radiata is a boreal to arctic species whose center of abundance in the western Atlantic extends northward from the Gulf of Maine probably as far as the Gulf of St. Lawrence. It

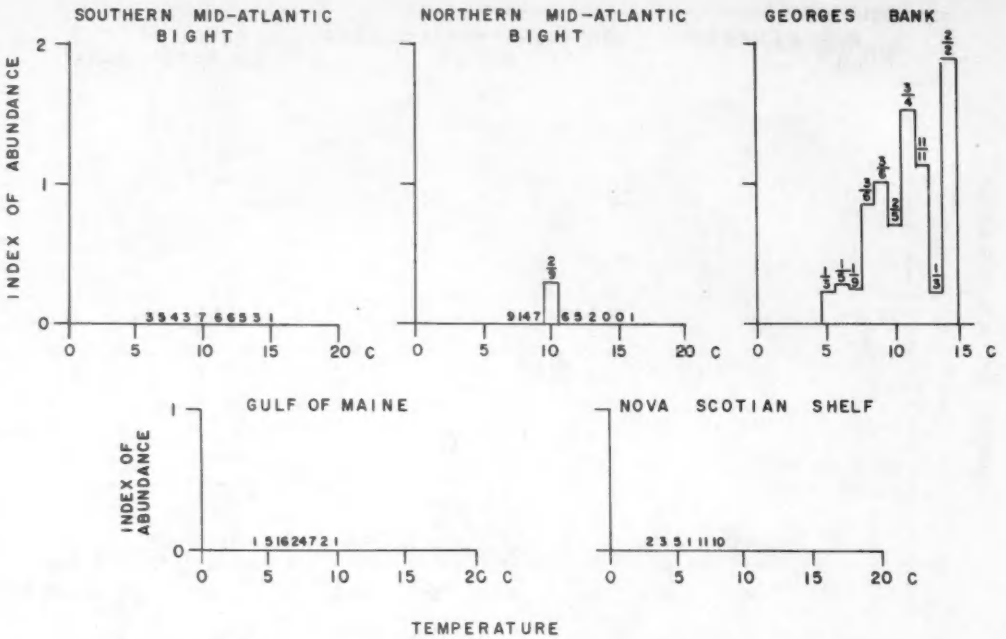

FIGURE 13.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

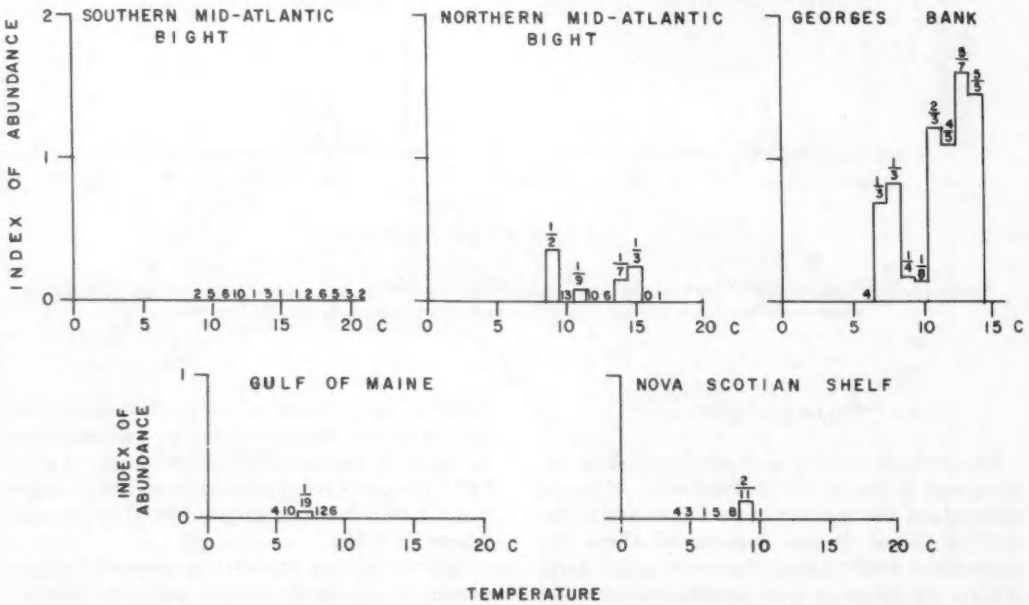

FIGURE 14.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

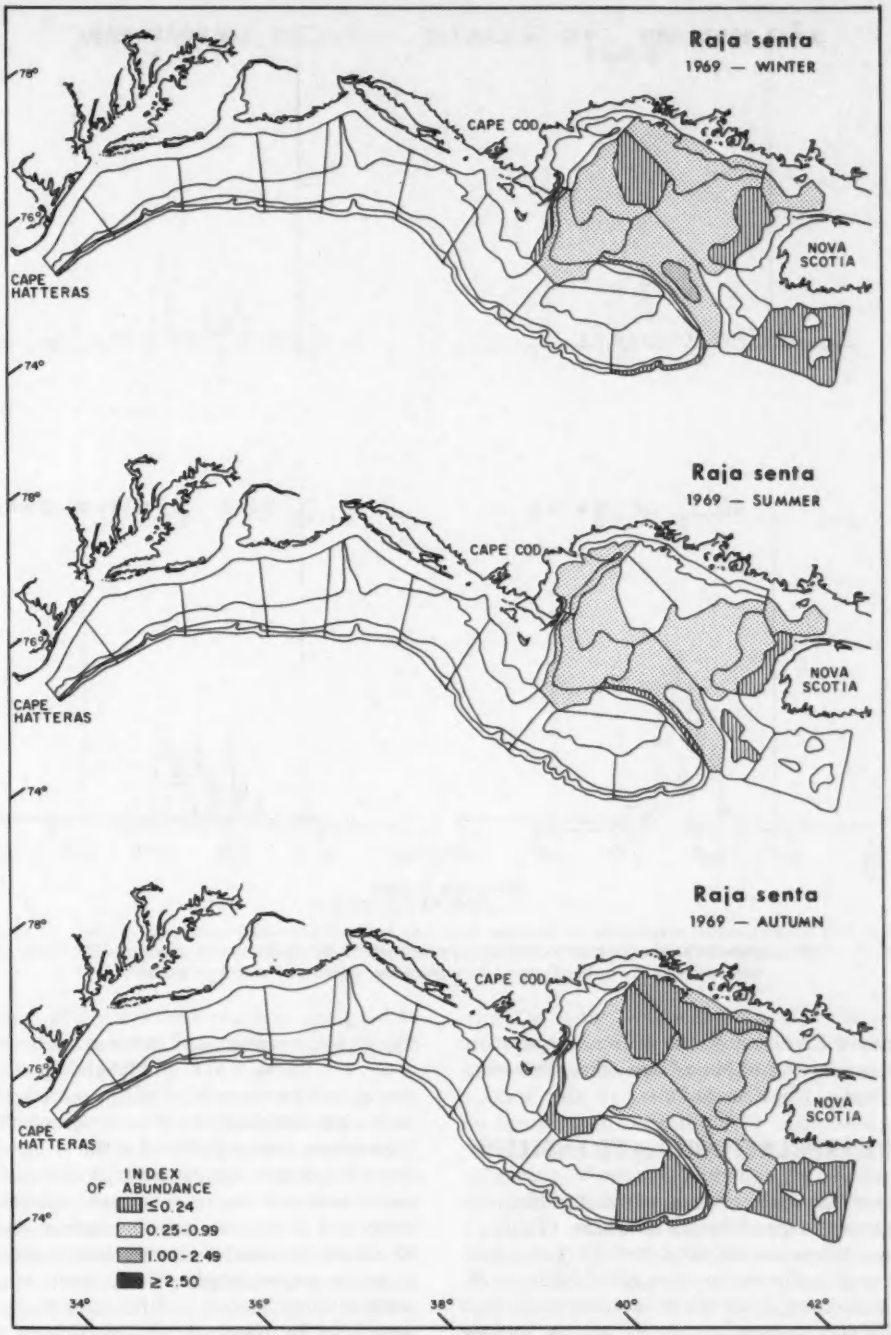

FIGURE 15.—Index of abundance (geometric mean) of *Raja senta* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

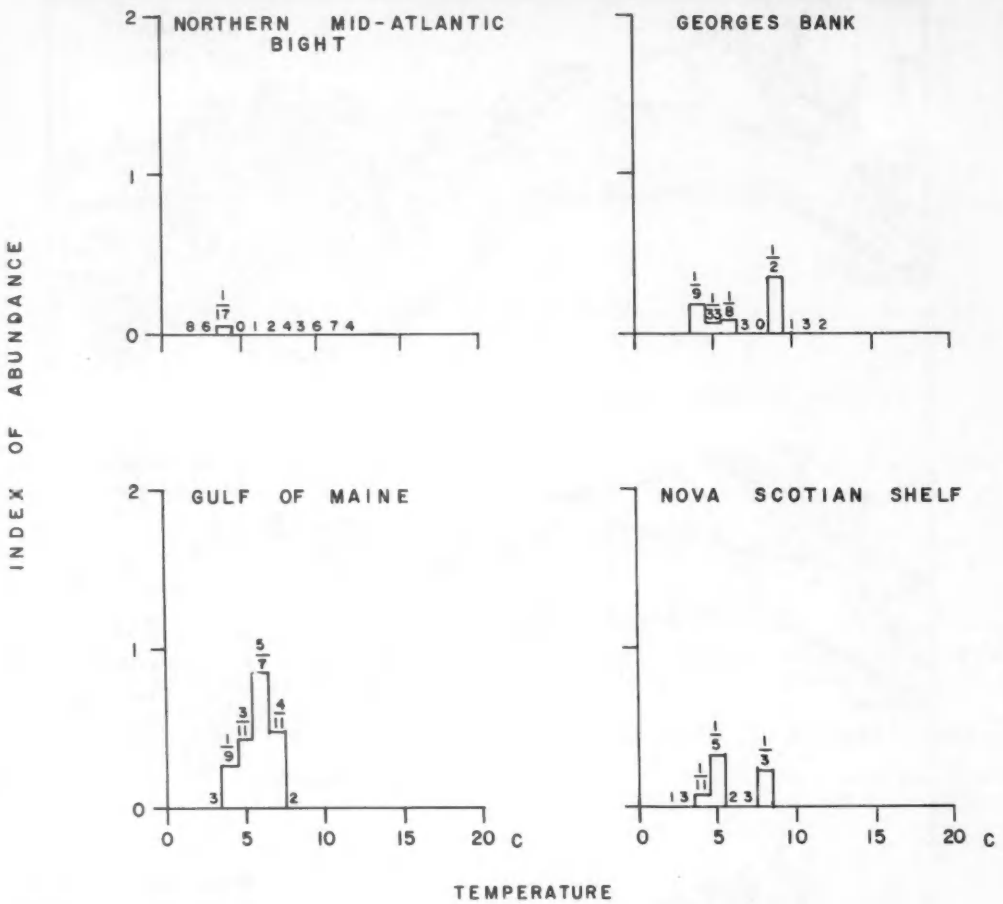

FIGURE 16.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

was found over almost the entire temperature range in the Gulf of Maine and off southeastern Nova Scotia. (Figures 20-22).

INTERSPECIFIC RELATIONSHIPS

Five of the species cooccurred significantly with one or more of the other species (Table 3). *Raja laevis* was associated with both *R. erinacea* and *R. ocellata* for half or more of the *Albatross IV* cruises. *Raja erinacea* and *R. ocellata* cooccurred significantly during all of the survey cruises and were positively associated by abundance. The product moment coefficients for the *Albatross IV* winter, summer, and autumn cruises of 1969 were: $r = 0.656$, 0.471, and 0.640. Percent of the variation in y associated with x was: 43%, 22%, and 41% respectively. The slopes of all three regressions were significant at the 1% probability level. No reason was apparent for the low correlation obtained during the summer cruise. *Raja senta* and *R. radiata* had the highest coefficient of association, and these two species were often negatively associated with *R. erinacea* and *R. ocellata*. *Raja senta* and *R. radiata* were not correlated by numbers; the coefficients for the *Albatross IV* winter, summer, and autumn cruises of 1969 were: 0.310, 0.081, and 0.283. Only a

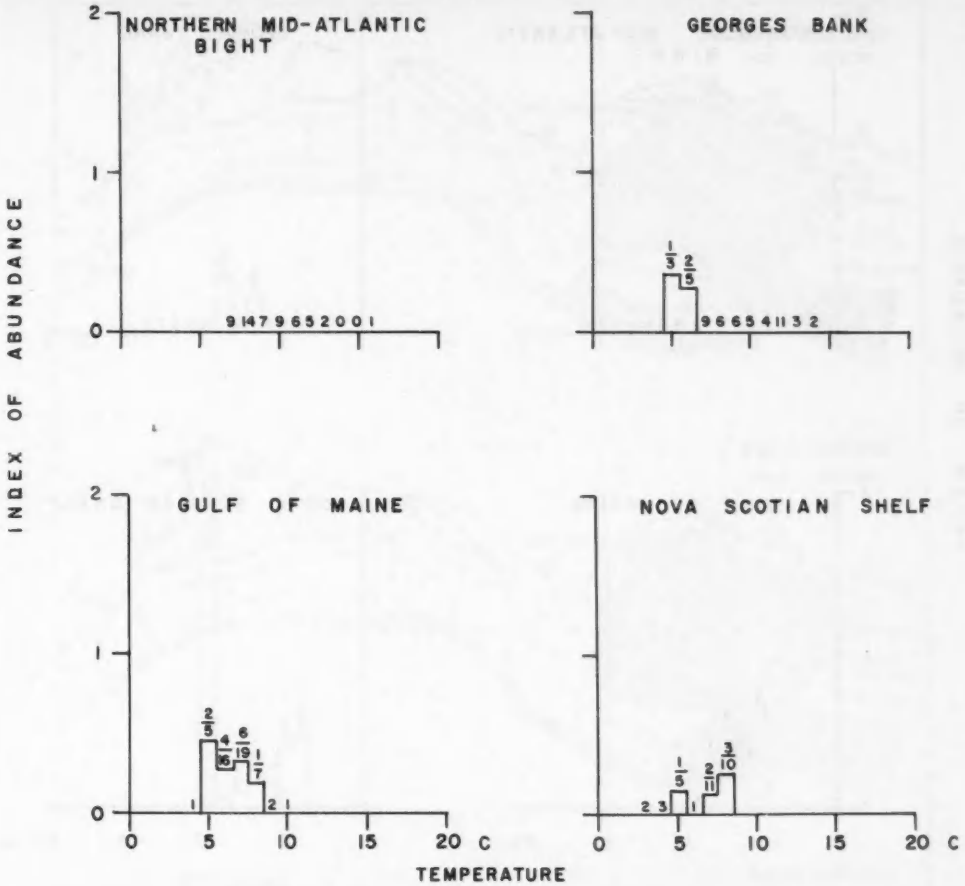

FIGURE 17.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

small part of the variance could be assigned to the correlation, and the slopes were not significant at the 5% probability level.

Raja erinacea and *R. ocellata* are predominantly found at depths less than 111 m in areas which, according to Uchupi (1963) are covered with sand or gravel. They have similar responses to seasonal temperature changes. In the southern periphery of their ranges they move southward during the colder months of the year and offshore and northward during the warmer months of the year. Within their centers of abundance, neither species undergoes a seasonal migration, each being able to tolerate the seasonal temperature extreme. *Raja ocellata* appears to have a slightly lower temperature preference as suggested by the difference in latitudinal distribution of the species. The apparent rareness of the species pair in the Gulf of Maine may be due to insufficient sampling. The shallowest depth zone (27-55 m) was not sampled during the *Albatross IV* cruises. Although the species have similar habitat requirements their positive correlation by numbers suggests that they are not competing for the same resources. Also a study of the food habits of the two species indicates that *R. erinacea* feeds largely on epifaunal organisms, and *R. ocellata* predominately selects infaunal organisms (McEachran 1973).

Raja laevis is found in the same areas as the

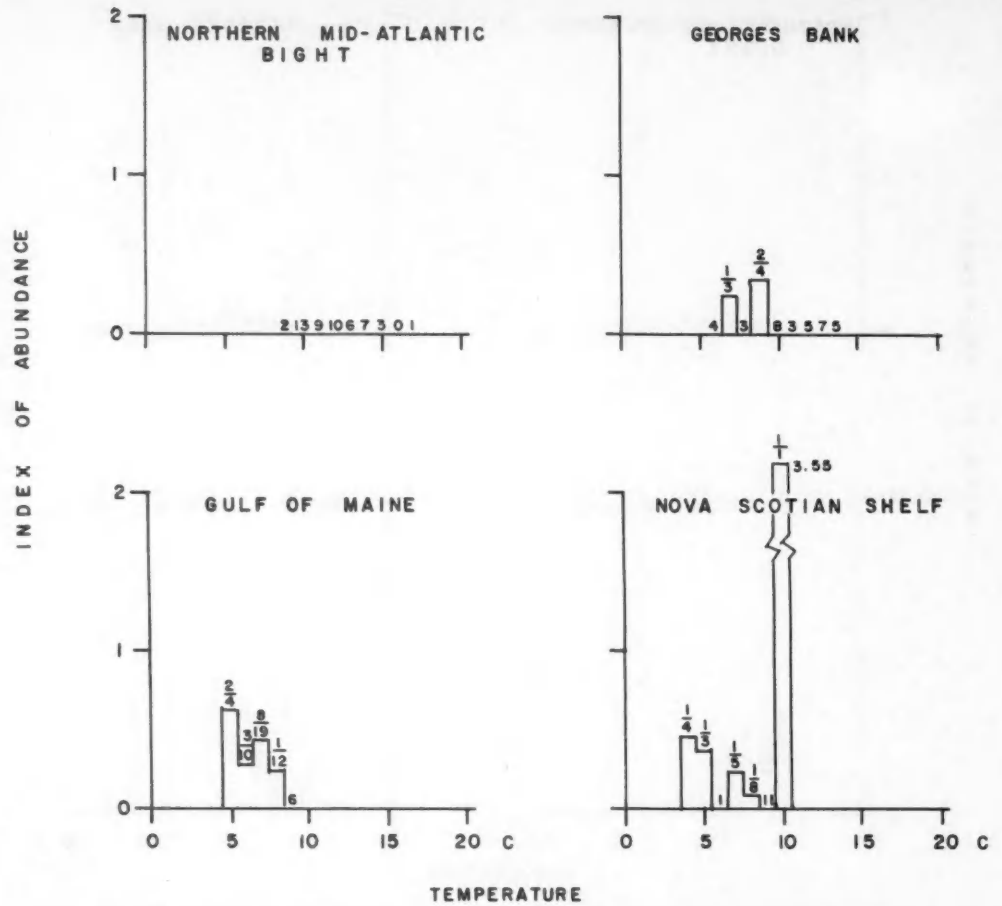

FIGURE 18.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

above species pair but has wider substratum and depth tolerance. Its low abundance may in part be explained by its considerably larger maximum size (Bigelow and Schroeder 1953) which makes it less available to the sampling gear.

The distribution of the *R. senta-R. radiata* species pair complements that of the *R. erinacea-R. ocellata* species pair. The former is found predominately in areas which, according to Uchupi (1963), were covered with sandy silt to silt and clay. They are taken over a narrower and lower temperature range than *R. erinacea-R. ocellata* and generally occur below 110 m. In the southern periphery of their ranges they are limited to a narrow band on the continental slope where the waters are thermally stable (Bigelow, 1933). Neither species appears to make seasonal movements. *Raja radiata* appears to have a wider temperature range and a lower temperature preference, and it is the more abundant of the two. The low abundance of *R. senta* may explain the lack of a positive or negative correlation by numbers between the species.

SUMMARY

Below the geographical, temperature and depth distribution of each species, based on literature

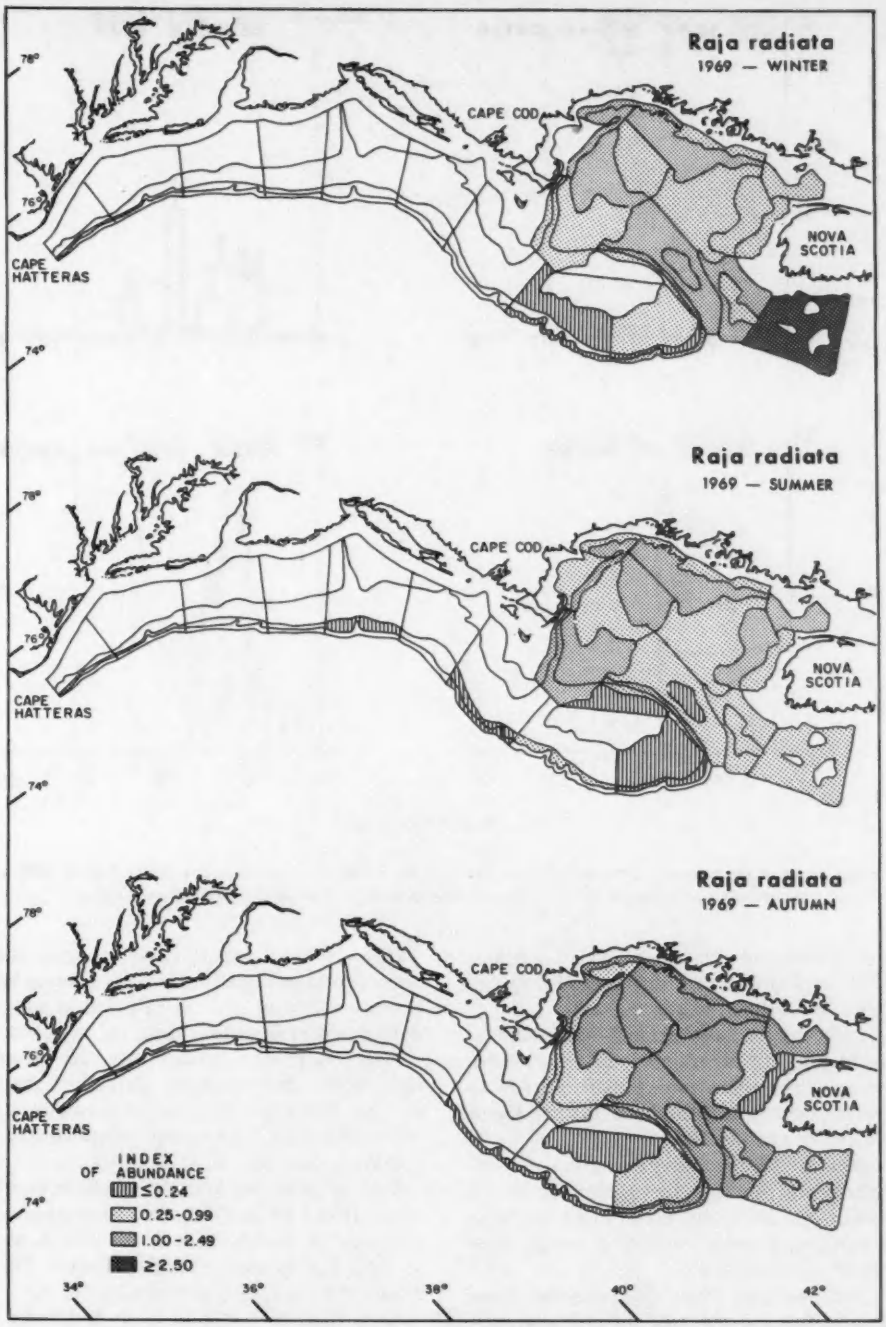

FIGURE 19.—Index of abundance (geometric mean) of *Raja radiata* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

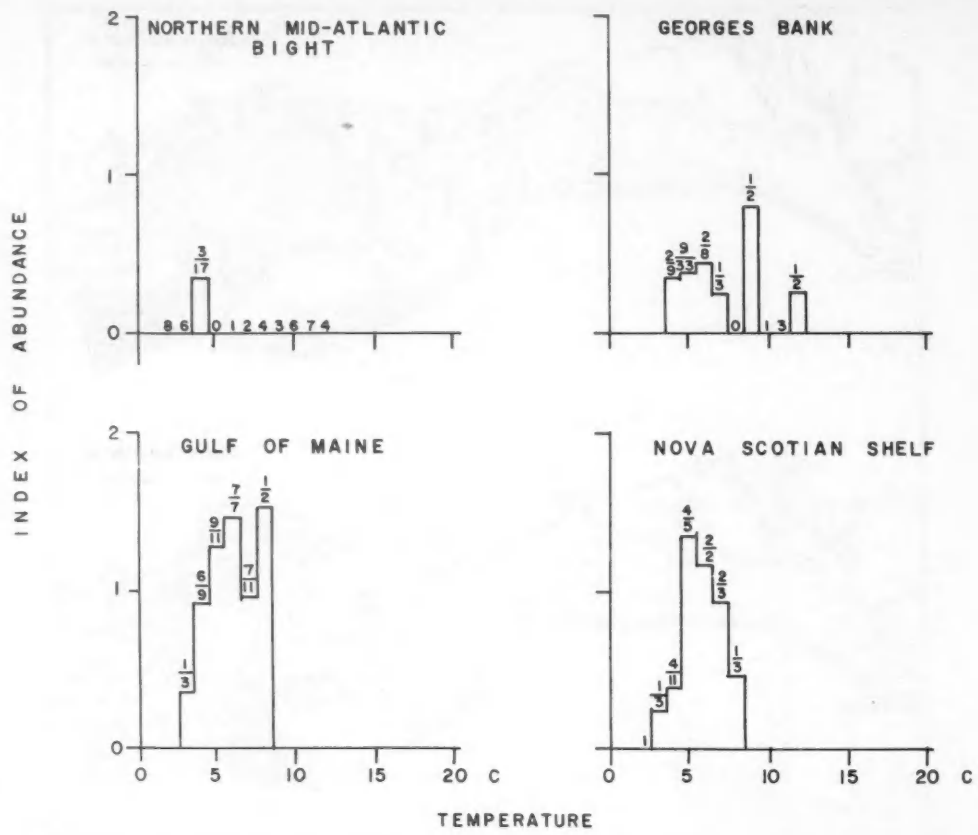

FIGURE 20.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

reports (Bigelow and Schroeder 1953; Leim and Scott 1966; and McEachran 1973) and findings in the present study, are summarized.

Raja eglanteria is found from Long Island to northern Mexico but is rare off southern Florida. It occurs from the shore zone to 329 m at 5° to 27°C, but is most abundant between the shore zone and 111 m at 9° to 20°C.

Raja garmani occurs from the offing of Nantucket Shoals to the Dry Tortugas, Fla. North of Cape Hatteras, N.C., it is found in 37 to 366 m at 6° to 17°C, and south of there it occurs from 66 to 366 m at 11° to 19°C.

Raja laevis extends from the southern Newfoundland banks and the Gulf of St. Lawrence south to North Carolina. It is found from shore to 750 m at 1.2° to 20°C.

Raja erinacea regularly occurs from southern Nova Scotia to Cape Hatteras. It is found between shore and 384 m at 2° to 21°C but is most abundant in water shallower than 111 m at 2° to 15°C.

Raja ocellata is found from the Newfoundland banks and southern Gulf of St. Lawrence to Cape Hatteras. It occurs from shore to 371 m at −1.2° to 19°C but is most abundant in water shallower than 111 m at 2° to 15°C.

Raja senta occurs from the southern Newfoundland banks and the Gulf of St. Lawrence to South Carolina. It occurs from 31 to 974 m at −1.3° to 14°C but is most abundant below 110 m at 2° to 10°C.

Raja radiata extends from Labrador, west Greenland, Hudson Bay, Grand Banks, and Gulf of St. Lawrence to South Carolina. It occurs from

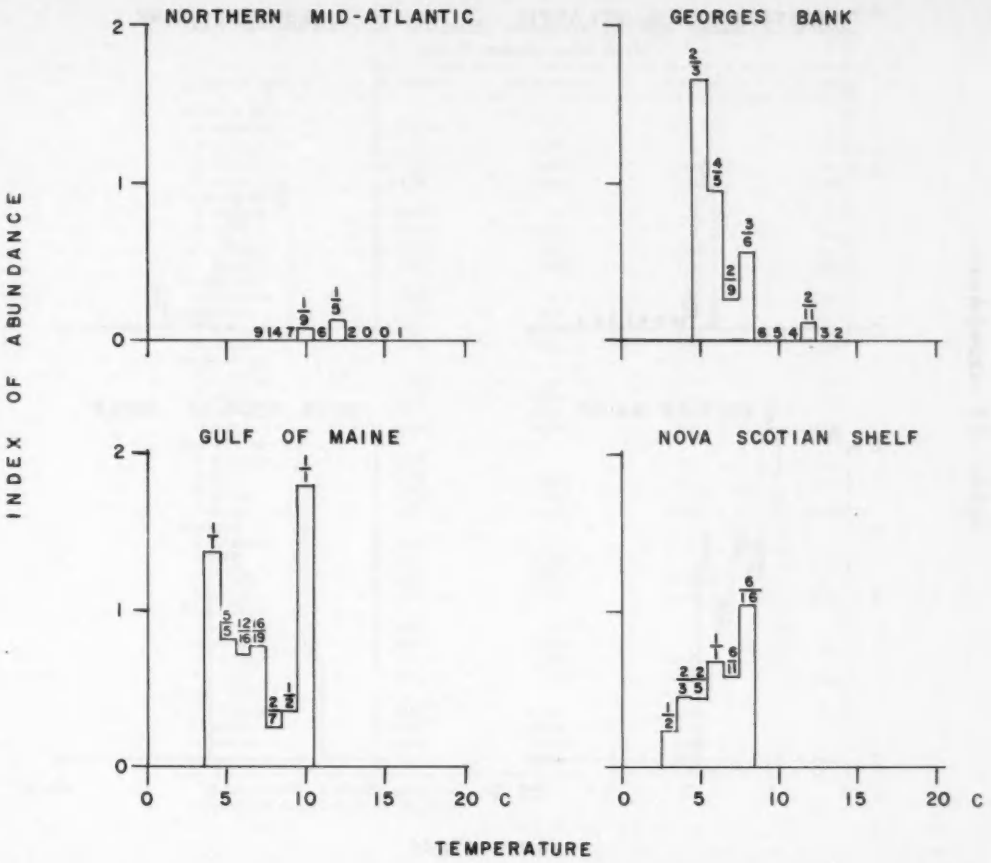

FIGURE 21.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

18 to 996 m at −1.4° to 14°C but is most abundant below 110 m at 2° to 10°C.

Raja erinacea and *R. ocellata* are sympatric species with very similar habitat requirements. *Raja ocellata* has slightly lower temperature preferences than *R. erinacea* and occurs farther to the north than the latter. *Raja senta* and *R. radiata* are sympatric species; *R. radiata* has wider temperature range and is more widespread than *R. senta*.

ACKNOWLEDGMENTS

We are very grateful to the Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA; the Fisheries Research Board of Canada Biological Station at St. Andrews, New Brunswick; and the Southeast Fisheries Center Pascagoula Laboratory, NMFS, NOAA for furnishing data for this study. The two former institutions also permitted the senior author to take part in their groundfish surveys.

The Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA gave access to their computer programs and computer facilities to summarize data. The VIMS survey of Chesapeake Bight was supported in part by the NMFS under P.L. 88-309, Project 3-5-D, Jackson Davis, Principle Investigator.

Special thanks is given to Marvin Grosslein of the Northeast Fisheries Center Woods Hole

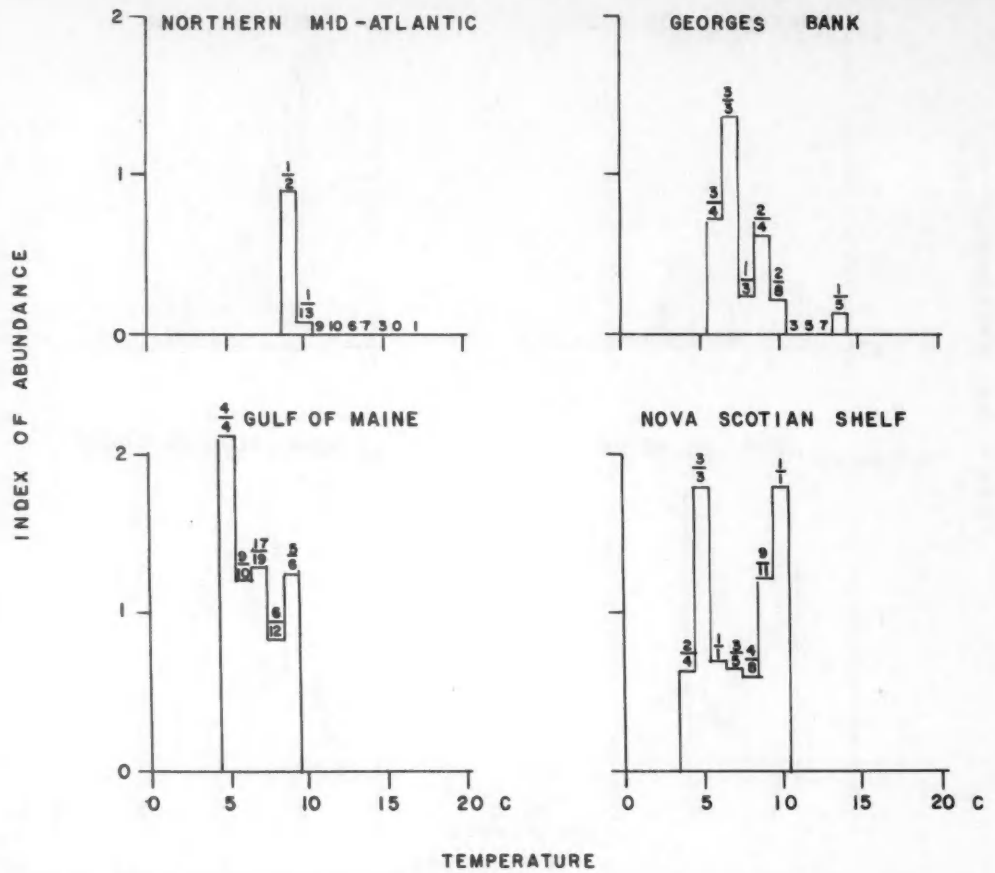

FIGURE 22.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Laboratory, NMFS, NOAA for his cooperation during all phases of this study. John B. Colton, Jr., also of the Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA supervised the construction of the isotherm charts. The following VIMS staff members and students contributed greatly to this study: Mark E. Chittenden and George C. Grant reviewed the manuscript; Russel L. Bradley and Kay Stubblefield did the drafting; Ken Thornberry did the photographic work; and Charles Wenner, Linda Mercer, Ken Able, Doug Markle, and Jim Weaver assisted with data collection.

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TABLE 3.—Coefficients of interspecific association for *Raja ocellata*, *R. erinacea*, *R. senta*, *R. radiata*, and *R. laevis*.

Cruise and species	*R. ocellata*	*R. erinacea*	*R. senta*	*R. radiata*
Cruise 67-21:				
R. erinacea	0.61**	—	—	—
R. senta	−0.02	−0.71	—	—
R. radiata	−0.28	−0.53**	0.60**	—
R. laevis	−0.02	0.00	0.00	0.00
Cruise 68-03:				
R. erinacea	0.67**	—	—	—
R. senta	0.00	0.00	—	—
R. radiata	−0.04	−0.32	0.84**	—
R. laevis	0.25*	0.53**	0.00	0.27
Cruise 68-17:				
R. erinacea	0.52**	—	—	—
R. senta	0.00	0.00	—	—
R. radiata	−0.85**	−0.54**	0.78**	—
R. laevis	0.14	0.45	0.00	0.00
Cruise 69-02:				
R. erinacea	0.63**	—	—	—
R. senta	−0.35	−0.34	—	—
R. radiata	−0.31	−0.23	0.95**	—
R. laevis	0.54**	0.36	−0.01	−0.03
Cruise 69-08:				
R. erinacea	0.71	—	—	—
R. senta	0.00	−0.62**	—	—
R. radiata	−0.56*	−0.42*	0.75**	—
R. laevis	0.72**	0.84**	−0.09	−0.02
Cruise 69-11:				
R. erinacea	0.57**	—	—	—
R. senta	−0.70	−0.85*	—	—
R. radiata	−0.21	−0.54**	1.00**	—
R. laevis	0.48	0.79**	0.00	0.34
Cruise 70-03:				
R. erinacea	0.53	—	—	—
R. senta	−0.01	−0.42	—	—
R. radiata	−0.12	−0.38	1.00**	—
R. laevis	0.13	0.47*	−0.09	0.01
Cruise 70-06:				
R. erinacea	0.41**	—	—	—
R. senta	−0.82**	−0.84**	—	—
R. radiata	−0.61**	−0.44**	0.80**	—
R. laevis	0.01	0.01	0.00	0.51

*Significant at the 0.05 probability level.
**Significant at the 0.01 probability level.

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THE GENERAL FEEDING ECOLOGY OF POSTLARVAL FISHES IN THE NEWPORT RIVER ESTUARY[1]

MARTIN A. KJELSON, DAVID S. PETERS, GORDON W. THAYER, AND GEORGE N. JOHNSON[2]

ABSTRACT

Food preferences, feeding intensity and chronology, evacuation rates, and daily rations were determined for postlarval stages of Atlantic menhaden, *Brevoortia tyrannus* (25-32 mm); pinfish, *Lagodon rhomboides* (16-20 mm); and spot, *Leiostomus xanthurus* (17-24 mm). Four copepod taxa, *Centropages, Temora, Acartia,* and Harpacticoida, made up 76-99% of the total gut contents. Postlarval feeding intensity was greatest during early daylight hours. Postlarval menhaden lost an estimated 60% of their orginal gut contents due to the stress of handling and capture. Similar stress caused no food loss in either postlarval pinfish or spot. Gastrointestinal evacuation of copepods and *Artemia* nauplii were described by linear regression. Evacuation rates varied directly with the amount of food in the gut. Rate constants were used in conjunction with information on the chronology of gut contents to determine daily rations. Daily ration estimates as a percent of the fish's wet body weight were: menhaden, 4.9%; pinfish, 3.5%; spot, 4.3% and 9.0%. The ration estimates for spot in terms of calories per fish per day were similar to the metabolic needs estimated from oxygen consumption measurements but were lower than the estimates from oxygen consumption for menhaden and pinfish.

Larval and postlarval fish are significant consumers in aquatic ecosystems, yet our knowledge of their feeding habits and daily food consumption is incomplete. This paper deals with the general feeding ecology of the postlarval stages of three common estuarine fishes. Four major aspects are discussed. These include 1) food preferences, 2) feeding intensity and chronology, 3) evacuation rate, and 4) daily ration.

Postlarval Atlantic menhaden, *Brevoortia tyrannus*; pinfish, *Lagodon rhomboides*; and spot, *Leiostomus xanthurus*, were collected during March of 1972 and 1973 from the Newport River estuary, Carteret County, N.C. The fish (hereafter referred to as larvae) were taken near Pivers Island, approximately 2.5 km inside the Beaufort Inlet. Pinfish and spot were collected using a seine and dip nets, while menhaden were captured in a channel net (Lewis et al. 1970) and with dip nets. One additional group of samples was collected in bongo nets. Most fish were frozen immediately following capture, thus stopping their digestive processes. The only exceptions to preservations by freezing were the bongo net samples which were placed in 5% Formalin.[3]

Food preferences were determined by examining the contents of entire digestive tracts. The gut contents from 120 fish of each species collected throughout the day were combined and individual food items identified, counted, and measured. Copepodite and adult copepods composed 99-100% (by both number and volume) of the identifiable food items in the digestive tracts. The average-sized copepod fed upon by each larval species was determined by measuring 100 copepods chosen from the combined digestive tract contents of all larvae collected in a 24-h period.

Diel periodicity of digestive tract contents indicated the intensity and chronology of feeding by the larvae. Twenty fish of each species were collected at 4-h intervals for 24 consecutive hours.

Larval evacuation rates for copepods and for *Artemia salina* were determined from laboratory experiments performed at 15°-17°C and 25-30‰; conditions which typify larval collection sites during March. Copepod evacuation was determined by collecting larvae from the estuary, placing them in food-free seawater tanks, and observing the decrease in their gut contents through time. At the time of initial capture

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and every 3 or 4 h thereafter, at least 10 fish were killed and the copepods present were counted. Evacuation of newly hatched *Artemia* nauplii was measured by allowing unfed larvae to feed to satiation on high prey densities (0.3 to 3.0 nauplii/cm^3), placing them in a food-free environment, and then periodically removing larvae for determination of remaining gut contents. Sampling of both copepod- and *Artemia*-fed fish continued periodically from the time of feeding until more than one-half of the fish had empty tracts.

Linear regression equations of log-transformed data were used to describe the evacuation process (Peters et al. 1974). The equations were of the form:

$$\log_{10} C = A + Bt$$

where C = 1 + the mean number of copepods or *Artemia* present in the gut
t = time
$A + B$ = regression terms

Instantaneous evacuation rates were calculated from the equation $\frac{dC}{dt} = 2.303\ BC$ (Peters and Kjelson in press).

Daily rations were calculated using information on diel periodicity of gut content and instantaneous evacuation rates. Previous calculations of fish rations (Bajkov 1935; Seaburg and Moyle 1964) have assumed a constant evacuation rate, but more recent data (Tyler 1970; Elliot 1972) indicate that digestive rate changes with the quantity of food in the digestive tract.

Our method of calculating daily ration (Peters and Kjelson in press) accounts for changes in evacuation rate which accompany diel changes of feeding intensity. To calculate the rations, we first determined an average instantaneous evacuation rate (in copepods per hour) for each of the 4-h sampling periods in the diel cycle. This average rate was the geometric mean of the instantaneous evacuation rates at the beginning and end of the period. Since each period lasted 4 h, the estimate of food evacuated during the period was four times the average instantaneous hourly evacuation rate. The total food evacuated per day was achieved by summing the six 4-h evacuation estimates, and is an estimate of the daily ration, because average ingestion rate must equal the rate at which material leaves the gut whether by assimilation or expulsion.

Daily rations were calculated initially as copepods per fish per day and then transformed to percent of the larval body weight and calories per fish per day. Dry weights of ingested copepods were estimated from the length-weight relationship:

$$W = 6.274L - 0.153$$

where W = dry weight in micrograms
L = copepod length, based on Heinle's (1966) data for all stages of *Acartia tonsa*

Copepod dry weights were converted to wet weights using a factor of 9.1 based upon our measurements of the wet/dry ratio for zooplankton, and were compared to wet weights of the fish to compute the daily ration as a percent of live body weight. Daily caloric intake was computed using our estimation of 0.555 cal/mg wet weight of an average size copepod during March, based on microbomb calorimeter measurements of mixed estuarine zooplankton (Thayer et al. 1974).

FOOD PREFERENCES

The larvae we collected were feeding primarily upon copepods, a common food source for both freshwater and marine fish larvae (Werner 1969; May 1970). Copepods composed 99% (by volume and number) of the gut contents of larval spot, pinfish, and menhaden (Table 1). Four copepod taxa (*Centropages, Temora, Acartia,* and Harpacticoida) were dominant. Diatoms, amphipods, barnacle larvae, crab zoea, and ostracods, although present in some larvae, were rare.

TABLE 1.—Relative (percent) composition by number of the major taxa in the total gut contents of three species of larval fish.

Taxa	Larval species		
	Pinfish	Spot	Menhaden
Harpacticoida	32	32	22
Centropages	28	28	40
Temora	3	21	6
Acartia	13	8	30
Other copepods	23	10	1
Other organisms	1	1	1
Total	100	100	100

Prey size is an important factor in determining the individuals selected by planktivorous fish (Ivlev 1961; Brooks and Dodson 1965; Kjelson 1971). The larval fish we studied appeared to restrict the majority of their feeding to items of a size ranging between 300 and 1,200 μm. Our observations of the mean length of ingested copepods showed that the larger menhaden larvae (26-31 mm, $\bar{x}$ = 29 mm TL) ingested 750-μm copepods with an estimated copepod wet weight of 0.04 mg, while the smaller spot (17-22 mm, $\bar{x}$ = 19 mm TL) and pinfish larvae (16-20 mm, $\bar{x}$ = 18 mm TL) fed upon 600-μm copepods with an estimated wet weight of 0.03 mg. Small zooplankters such as copepod nauplii, barnacle larvae, or small adult copepods such as *Oithona* (all present in the plankton tows) were rarely found in gut contents. Copepods larger than 1.2 mm were in the plankton, but were rarely consumed. Perhaps copepods were the only food items of the appropriate size present in sufficient abundance. Had we collected smaller larvae, it is possible food preferences may have been for smaller food items such as copepod nauplii and copepodites and adults of small-sized species as well as phytoplankton. May (1970) stressed the fact that larval fish require progressively larger prey as they grow. However, since larvae smaller than the size we collected are rarely found in the Newport River estuary, we feel our data indicates that smaller planktonic forms are relatively unimportant to the larval fish studied in this estuary.

Thayer et al. (1974) found that as a yearly average, copepods represented 81% of the zooplankton numbers and 85% of the zooplankton biomass retained by a No. 10 mesh plankton net. Since larval fishes enter the Newport River estuary during winter and spring, the consumption of copepods by these three larval species may, in part, explain the decrease in copepod abundance observed by Thayer et al. (1974) during this period. They noted that the four copepod taxa utilized by these larvae decreased from a mean of 81% of the copepod biomass during March 1970 and 1971 to a mean of 48% of the biomass during the summer.

FEEDING CHRONOLOGY AND INTENSITY

All three larval fishes had the highest food content in their digestive tracts during daylight hours (Figures 1-3). Periodicity of gastrointestinal contents indicates that each population begins feeding near dawn and reaches a maximum gut fullness near midday. The rapid single increase in the gut content of the three species indicates they have one major burst of feeding activity per day (Figures 1-3). Other studies (Blaxter 1965; Schumann 1965; Braum 1967; June and Carlson 1971) have shown that larval fish generally do not have food within their digestive tracts when captured at night, suggesting that larval fish do not feed at low light intensities.

Considerable variation was observed in the amounts of food present in larval guts (Figures 1-3). The variation is probably due to differences in prey abundance or capture and handling techniques, although other factors such as fish size and copepod size may also be important. During our 24 h sampling the variation in numbers of copepods in individual fish was high at some times and low at others. The ratio of the standard error of the estimate to the mean varied from 4 to 48% for spot with a mean of 21%; for menhaden the ratio varied from 0 to 100% with a mean of 40%; and for pinfish it varied from 0 to 100% with a mean of 43%. Spot larvae

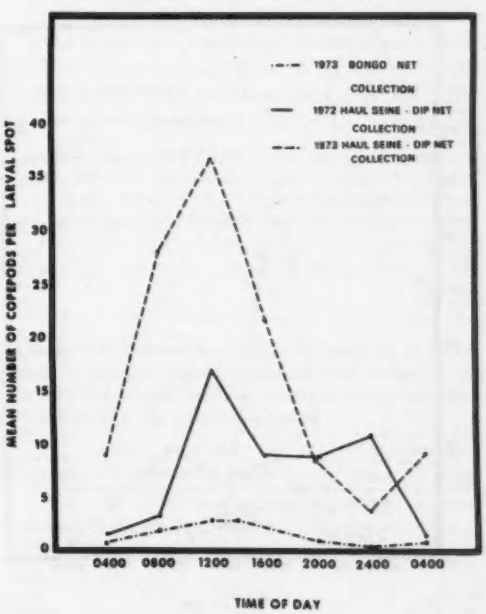

FIGURE 1.—Variation in diel cycle of gastrointestinal contents in postlarval spot.

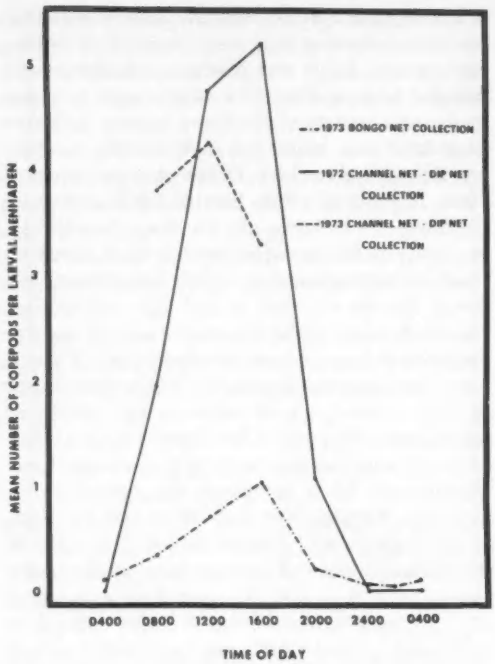

FIGURE 2.—Variation in diel cycle of gastrointestinal contents in postlarval Atlantic menhaden.

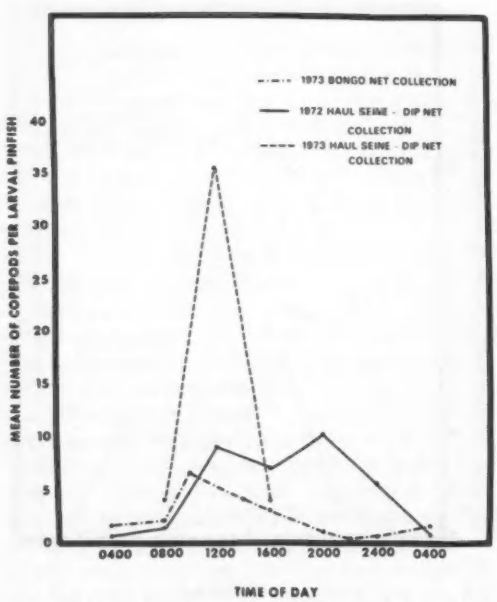

FIGURE 3.—Variation in diel cycle of gastrointestinal contents in postlarval pinfish.

(18-24 mm, $\bar{x}$ = 21.5 mm) collected by dip net at one location and between 0830 and 1030 h over a 4-day period had little variation in their mean gut contents. Spot larvae collected 2 April averaged 25.3 copepods/fish (SE = 2.3), on 3 April, 21.3 (SE = 2.0), and on 5 April, 26.3 (SE = 3.7). The similarity of food quantity in the larval digestive tracts suggests that prey abundance may have remained relatively constant over the 4-day period thus allowing the fish to consume similar amounts of food.

ESTIMATES OF LARVAL GUT CAPACITIES

Laboratory feeding experiments were conducted at 15°-16°C to estimate the maximum gut capacity of the larvae. The fish were fed high densities of *Artemia* nauplii until their digestive tracts were completely packed from esophagus to anus. Menhaden (28-32 mm, $\bar{x}$ = 30 mm TL) fed for 20 min on a concentration of *Artemia* nauplii, 3 nauplii/cm^3, had an average of 145 nauplii/fish in their digestive tracts (SE = 9.6). Spot larvae (19-23 mm, $\bar{x}$ = 21 mm TL) fed for 15 min on 0.3 nauplius/cm^3 had an average of 89 (SE = 7.0) nauplii/fish; and pinfish (16-20 mm, $\bar{x}$ = 18 mm TL) fed for 1 h on 0.3 nauplius/cm^3, had an average of 75 (SE = 15.1) nauplii/fish. By comparing individual *Artemia* and copepods of the four major taxa side by side under a microscope, we estimated that the volume of two 450-μm *Artemia* nauplii were equivalent to that of one 650-μm copepod. Using 0.5 as a conversion factor, we calculated maximum gut capacities in terms of copepods. Menhaden larvae of 30 mm have a gut capacity of 72 copepods, 21-mm spot a gut capacity of 44 copepods, and 18-mm pinfish a gut capacity of 37 copepods. These estimates of gut capacity were comparable to the maximum numbers of copepods observed in the digestive tracts of larval fish collected in the estuary for spot (36.5 copepods/fish) (Figure 1) and pinfish (35.3 copepods/fish) (Figure 3), but not for menhaden (5.2 copepods/fish) (Figure 2). This large difference between gut capacity and observed gut contents suggests that menhaden larvae either feed very little under natural conditions, and never approach the estimated maximum gut capacity or capture and/or handling causes them to regurgitate or defecate causing inaccuracy in our estimate of natural gut content. To test

the latter possibility, we performed a variety of experiments to determine if handling and capture technique influences the quantities of food observed in the larval gut.

EFFECTS OF SAMPLING TECHNIQUE ON GUT CONTENT

Larvae of all three species were first collected by a 3-m channel net with an attached live box. Captured fish were counted, identified, divided into two groups, and transferred (underwater) into separate containers. One group of fish was anesthetized with 0.12 g/liter MS-222 (tricaine methanesulfonate) and then dissected, while the other group was transferred carefully into the posterior end of a 20-cm bongo net (keeping them underwater throughout transfer). The net was towed for 5 min, and after retrieval the larvae were removed, identified, and counted to assure that none were lost and that no new larvae were captured. The fish were then dissected to determine the number of copepods present in their guts. Menhaden lost 68% of their gut contents when exposed to the stress of bongo tows, whereas gut contents of larval spot and pinfish before and after the bongo tow did not differ statistically (Table 2). The amounts of food present in all three species of larvae collected at the Beaufort Inlet in the 24-h bongo samples were lower than the food quantities observed in larvae collected by the other techniques inside the estuary (Figures 1-3). Thus, factors other than the stress of capture may be responsible for the low gut contents in larvae collected in the bongo nets: 1) copepod abundance may have been lower at the Beaufort Inlet sampling site than further inside the estuary, 2) the use of Formalin (restricted to bongo samples) to kill and preserve the larvae may have caused defecation of the copepods prior to analysis (June and Carlson (1971) showed that larval menhaden when placed in Formalin had violent spasms accompanied by defecation), and 3) larvae collected in midchannel by bongo nets may not be feeding as actively since they are exposed to a greater tidal current (perhaps the protected inshore waters of the estuary may allow the larvae to feed more efficiently and result in fish with greater numbers of prey in their digestive tracts).

No significant differences were observed in the food contents of spot larvae collected by routine seining and those collected by seining with a more gentle sampling technique (Table 3). In routine seining, the larvae were picked out of the seine as it lay on the shore and placed in a bucket of ice water. The gentle sampling technique consisted of surrounding a body of water with the seine and then concentrating the larvae, taking care that fish were not forced against the net. Once concentrated, the larvae were dipped out of the water in a bucket and anesthetized with MS-222. The results of our sampling experiments indicate that routine field sampling techniques used to collect spot and pinfish larvae probably caused little loss of food from the digestive tracts.

EFFECTS OF HANDLING TECHNIQUE ON GUT CONTENT

In the laboratory, handling stress did not reduce the food quantities present in larval spot and pinfish, but did reduce the amount of food remaining in larval menhaden (Table 4). Two groups

TABLE 2.—The effect of bongo net tow stress upon the amount of food observed in larval menhaden, pinfish, and spot.

Capture technique	Menhaden[1]	Pinfish[2]	Spot[3]
	Mean number copepods/fish ± one SE		
Channel net	7.4 ± 2	1.3 ± 0.6	6.4 ± 4.4
Channel net + bongo net tow	2.4 ± 0.7	0.8 ± 0.3	7.0 ± 2

[1] n = 22 larvae.
[2] n = 18 larvae.
[3] n = 5 larvae.

TABLE 3.—Comparison of food quantities, mean number of copepods per fish ± one SE, present in larval spot (22-33 mm, $\bar{x}$ = 27 mm) collected by haul seine using rough and gentle handling techniques. Ten fish were collected per sample.

Date	Gentle	Rough
April 2	84.5 ± 7.4	78.6 ± 5.3
April 3	69.7 ± 5.9	66.9 ± 5.5

TABLE 4.—The effects of handling on the retention of *Artemia* nauplii in digestive tracts of larval Atlantic menhaden, pinfish, and spot. Rough handling is approximately equivalent to field capture by dip net and haul seine.

Species (Range mm)	Experiment 1		Experiment 2	
	Gentle	Rough	Gentle	Rough
	Mean number ± one SE			
Menhaden[1] (28-32)	71 ± 15	29 ± 10	145 ± 10	76 ± 11
Pinfish[2] (16-20)	37 ± 4	34 ± 5	35 ± 9	43 ± 6
Spot[2] (19-23)	51 ± 5	47 ± 5	89 ± 7	92 ± 10

[1] n = 18 larvae per sample.
[2] n = 36 larvae per sample.

of unfed larvae of each species were offered identical concentrations of *Artemia* nauplii. One group was handled roughly to represent the physical stress associated with field capture, while the other group was handled gently. The roughly handled fish were chased around the tank with a dip net for 10 to 30 s, captured with the net, allowed to suffocate in air, and then dissected. After feeding, the other fish were anesthetized by carefully adding an aqueous solution of MS-222 to the tank and then were dissected immediately to determine the numbers of nauplii in their digestive tracts. The roughly handled menhaden had only 40 to 52% of the *Artemia* numbers present in the guts of the gently handled menhaden (Table 4). The loss of food in menhaden larvae probably was due to the stress-related defecation or regurgitation and thus, may explain the consistently low quantities of food observed in larval menhaden captured in the estuary. Roughly handled pinfish and spot larvae showed no significant decrease in gut contents (Table 4). The curved digestive tract of larval spot and pinfish may prevent rapid passage of food, while the straight tubelike gut of menhaden may permit easy loss of food. This gut shape difference may account for the differences we observed.

A separate experiment was conducted to determine if the technique used to kill menhaden larvae in the handling experiments (exposure to air and suffocation versus anesthesia with MS-222) influenced the amount of food remaining in the gut. No difference was found. Fish killed by suffocation had a mean of 19 *Artemia* nauplii/fish (SE = 4.7), while fish anesthetized with MS-222 had a mean of 20 *Artemia* nauplii/fish (SE = 4.2).

EVACUATION RATES

Estimated regression coefficients for the equations describing the evacuation of copepods and *Artemia* nauplii are provided in Tables 5 and 6. Certain factors may alter the reliability of our estimates of evacuation rate under natural estuarine conditions. Bias may result from the temperature difference between estuarine waters from which fish were captured (14°-15°C) and the aquaria temperature during evacuation experiments (16°-17°C). The effect of a 2° temperature change on evacuation rate of larvae

TABLE 5.—Linear regressions describing evacuation of copepods in Atlantic menhaden, pinfish, and spot larvae. $Y = A + Bt$ where $Y = \log_{10}(1 + \text{mean number of copepods per larva})$ and t = hours since feeding. n = the number of data points.

Species	Mean TL (Range mm)	A	B	n	r^2	Temperature (°C)
Menhaden	29 (27-31)	1.14	−0.17	3	0.98	16
Pinfish	17 (15-20)	0.94	−0.10	3	0.86	16
Pinfish	16 (13-19)	0.68	−0.08	4	0.98	17
Spot	20 (17-23)	0.91	−0.10	5	0.98	17

is unknown, although a similar change significantly increases the evacuation rates in some juvenile marine fish (Peters and Kjelson in press). Although our regression model could probably be improved, the r^2 values (Tables 5, 6) indicate the model is reasonable. Initial analysis included data collected until all the fish were empty. This resulted in nonlinearity near the end of evacuation due to bias near the end of evacuation period where more weight was given to the slower evacuating fish. Thus, by including in the regression analysis data from only those samples in which at least half of the larvae contained some food, this bias was decreased and the linear regression model appeared to represent larvae evacuation adequately.

INFLUENCE OF HANDLING AND CAPTURE ON EVACUATION

Evacuation experiments using *Artemia* nauplii were performed to determine if handling and capture influenced the rate of evacuation. Each

TABLE 6.—Linear regressions describing evacuation of *Artemia* nauplii in Atlantic menhaden, pinfish, and spot larvae under varied handling conditions. $Y = A + Bt$ where $Y = \log_{10}(1 + \text{mean number of } \textit{Artemia} \text{ per larva})$ and t = hours since feeding. n = the number of data points.

Species	Mean TL (Range mm)	A	B	n	r^2	Handling condition	Temperature (°C)
Menhaden	29 (27-32)	2.36	−0.28	5	0.96	Gentle	15
Menhaden	29 (27-32)	2.04	−0.34	3	0.86	Rough	15
Pinfish	16 (14-18)	1.64	−0.26	4	0.97	Gentle	16
Pinfish	16 (14-17)	1.73	−0.28	3	0.92	Rough	16
Spot	20 (18-23)	2.12	−0.19	5	0.94	Gentle	16
Spot	20 (18-23)	2.11	−0.18	5	0.95	Rough	16

of the three larval fish species were fed concentrated amounts of *Artemia* (> 0.3 nauplius/cm^3) and allowed to feed until their digestive tracts were full. Each species then was transferred to food-free containers and separated into two groups, one handled roughly and another handled gently. Fish were sampled immediately and every 2 h thereafter. The rough treatment was similar to that used to study the influence of handling on gut content. The gently handled fish were sampled by dipping them carefully out of the tank with a beaker and anesthetizing them prior to dissection. The similarities of the regression coefficients (Table 6) for fish of the same species under the two treatments indicate that evacuation rates were not affected by rough treatment. The higher B value for roughly handled menhaden was not significantly different. Thus, our use of laboratory evacuation data to represent the normal evacuation in nature appears reasonable.

The regression coefficients for *Artemia* nauplii evacuation were larger (B values ranging from -0.18 to -0.34) than those for copepod evacuation (B values ranging from -0.08 to -0.17) for all three species (Tables 5, 6). This was expected since the *Artemia* nauplii were estimated to be only one-half the volume of copepods ingested by the larvae.

Food quality may also affect evacuation rate. Rosenthal and Hempel (1970) working with herring larvae found that *Artemia* nauplii were not digested as completely as copepods. We also observed that copepods become transparent in the posterior gut, whereas *Artemia* nauplii remained opaque.

The variation in the numbers of prey per larva between individual menhaden and pinfish larvae increased with each successive sampling period (0, 2, 4, 6, and 8 h after feeding stopped), but fluctuated in spot. The increasing variation in menhaden and pinfish may be explained by differences in individual evacuation rates. Food densities and gut capacities were relatively constant for the individual larva and thus, the initial numbers of prey per larva were similar. Varied individual evacuation rates would influence the amounts present in the tracts of the fish sampled at later times and therefore increase the variation. Individual fish may have significantly different evacuation rate constants as has been shown for juvenile pinfish (Peters and Hoss 1974).

DAILY RATIONS

The estimated daily rations for the three larval fish species varied between 3.5 and 9.0% of the mean wet weight of the fish or from 38 to 99 copepods/fish·day. The daily ration estimate for menhaden larvae (Table 7) was corrected by a factor of 2.5 to account for the fact that menhaden larvae lose approximately 60-68% of their gut contents during capture and subsequent handlings (Tables 2, 4). Since pinfish and spot larvae did not lose food from their gut when put under the stress, no correction factor was used.

Two estimates of daily ration, based upon both the 1972 and 1973 haul seine-dip net collections (Figure 1), are provided for spot larvae (Table 7). The two spot rations (4.3% and 9.0% of the body weight) differ considerably, probably due to differences in food availability.

Measurements of larval metabolic expenditures based on O_2 consumption (D. E. Hoss and W. F. Hettler, Jr., Atlantic Estuarine Fisheries Center,

TABLE 7.—Daily rations calculated from feeding studies and O_2 consumption measurements at 15°-17°C for larval Atlantic menhaden, pinfish, and spot in the Newport River estuary, N.C.

Species (range mm)	Mean larvae wet weight (mg)	Number copepods/ fish·day	Percent of body weight	Calories/ fish·day	Calories/fish·day estimated from O_2 consumption[1, 2]
1972:					
Menhaden (27-32)	43	53	4.9	1.18	3.0
Pinfish (16-20)	32	38	3.5	0.63	1.2
Spot (17-23)	33	47	4.3	0.78	1.2
1973:					
Spot (17-23)	33	99	9.0	1.65	1.2

[1]From Hettler and Hoss, unpubl. data.
[2]3.38 cal/mg O_2.

National Marine Fisheries Service, NOAA, pers. commun.) are higher than three of our four larval ration estimates (Table 7). Our menhaden ration of 1.18 calories/fish·day was 40% of the 3.0 calculated from Hoss and Hettler's measurements of respiration rate, indicating that for this species our estimate is probably low. Our pinfish ration was also lower, being 52% of that calculated from the O_2 consumption method. Our menhaden estimate is highly dependent on a very tentative factor used to adjust for handling effects. More accurate measurement of this conversion factor would probably provide better correlation with metabolic costs. Our 1972 spot ration was 66% of maintenance needs and may be indicative (as with pinfish and menhaden) of natural food shortages or environmental conditions not optimal for feeding on the dates of collection in 1972. The 1973 spot ration was nearly twice that estimated from O_2 consumption measurements and provides sufficient energy for general metabolism and growth.

We must consider our larval ration estimates as tentative in light of the high variability in the ration estimates for spot. This variation is due to differences in natural gut content, possibly as a result of differences in food availability on the sampling dates. Extensive sampling under the varied environmental conditions and zooplankton abundances and repeated evacuation rate measurements will provide us with more accurate estimates of their daily ration.

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THE LARVAL DEVELOPMENT OF PACIFIC *EUPHAUSIA GIBBOIDES* (EUPHAUSIACEA)

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ABSTRACT

The larval development of *Euphausia gibboides* is described and illustrated, including nauplius stages I and II, metanauplius stage, calyptopis stages I-III, and furcilia stages I-VI; dominant and variant forms, with respect to reduction in number of terminal telson spines, were found in furcilia IV-VI. Identification of developmental stages was substantiated by the study of a series of juveniles of *E. gibboides*, the largest of which had characters of both the furcilia phase and the adult. Larvae were studied in plankton samples from several areas within the range of the species in the Pacific Ocean; variation in size of calyptopes in different areas is described.

Euphausia gibboides Ortmann is a relatively large euphausiid of the temperate and tropical Pacific. It is closely related to *E. sanzoi* Torelli and *E. fallax* Hansen and with them forms a "*Euphausia gibboides* group" (Brinton 1962). In the North Pacific, *E. gibboides* is found in the transition zone between lat. 30° and 45°N and extending southward to about lat. 20°N in the east where it is considered a major species of the California Current system; in the South Pacific it occurs in the eastern equatorial zone. *Euphausia sanzoi* has been found in the Red Sea and western Indian Ocean, and *E. fallax* in the western tropical Pacific. The distributions of these species are discussed by Brinton (1962, 1967a, b, 1973), Brinton and Gopalakrishnan (1973), Roger (1967), and Mauchline and Fisher (1969). The distribution of the larvae of *E. gibboides* in the California Current is shown by Brinton (1967a, b, 1973).

Hansen (1911) divided the species of the genus *Euphausia* Dana into four groups with respect to armature of carapace and abdomen; of these, groups A and D were considered to be "well separated" but groups B and C "somewhat badly defined." Group C, the largest of the four, contains 12 of the 32 species now recognized in the genus: *E. mucronata*, *E. paragibba*, *E. pseudogibba*, *E. hemigibba*, *E. gibba*, *E. lamilligera*, *E. distinguenda*, *E. sibogae*, *E. gibboides*, *E. fallax*, *E. sanzoi*, and *E. vallentini* (*E. alvae* and *E. consuelae*, both considered difficult to evaluate are not included) (Boden et al. 1955). An early furcilia of *E. hemigibba* (Lebour 1949) and a late furcilia of *E. distinguenda* (Hansen 1912) have been identified, but a series of developmental stages has been described for only one of the group C species, *E. vallentini* (John 1936). In his investigation of the adults and larvae of the southern species of *Euphausia*, John has shown the affinity of *E. vallentini* and certain species of group B with which it may now be associated (Mauchline and Fisher 1969). Studies of the larvae of additional species should aid not only in identification of planktonic forms but also in definition of specific relationships within the genus.

The present paper provides descriptions of the developmental stages of *Euphausia gibboides*; it is part of a larger study whose purpose is to identify and describe larvae of the three species of the "*Euphausia gibboides* Group" and to compare the larval morphology of these closely related forms.

METHODS AND MATERIALS

Larvae of *E. gibboides* were obtained from preserved plankton samples in the Marine Invertebrate Collections of the Scripps Institution of Oceanography. They were sorted from net hauls, taken with the standard CalCOFI (California Cooperative Oceanic Fisheries Investigations) 1-m net (Ahlstrom 1954), which were known to contain larvae and juveniles of the species. The positions of these tows are given in Table 1; station data for the samples are given by Snyder

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TABLE 1.—The area, station number, and position of samples from which larvae of *E. gibboides* were obtained.

Area	Cruise	Station	Position (Lat., Long.)
North Pacific:			
Eastern	CalCOFI 6304	60.140	34°65.0'N, 129°19.5'W
	CalCOFI 6304	70.90	34°53.0'N, 125°13.0'W
	CalCOFI 6304	70.100	34°33.0'N, 125°13.0'W
	CalCOFI 6304	110.70	28°36.0'N, 118°18.0'W
	CalCOFI 6304	117.90	26°47.5'N, 118°50.0'W
	CalCOFI 6304	120.120	25°12.5'N, 120°22.5'W
	CalCOFI 6304	133.80	24°14.5'N, 116°17.5'W
	CalCOFI 6307	117.80	27°07.5'N, 118°06.0'W
Western	Transpac	56A + B	41°49.0'N, 166°38.6'E
	Transpac	76A	39°56.4'N, 143°38.5'E
Equatorial Pacific:			
Eastern	Shellback	187	1°39.5'N, 92°05.0'W
	Shellback	188	1°06.5'N, 93°14.5'W

and Fleminger (1965) and in University of California Data Reports (Scripps Institution of Oceanography 1964a, b).

The larvae were grouped by developmental phase, measured, and dissected for detailed study of appendages. The identification of eggs, nauplii, and metanauplius is based on their relative abundance in samples in which calyptopes and furcilia of *E. gibboides* were clearly the dominant euphausiid larvae. Identification of calyptopis and furcilia stages, based on morphology, distribution, and relative abundance with juveniles and adults of *E. gibboides*, was substantiated by the study of a series of juvenile forms the largest of which had characters of both the furcilia phase and the adult.

The identification of calyptopis I was confirmed by rearing after the manuscript had been accepted for publication. A gravid female of *E. gibboides*, caught in a mid-water trawl collection at lat. 27°35.5'N, long. 115°52.0'W, deposited her eggs soon after capture and larvae which hatched from the eggs were cultured through the first four developmental stages. I am indebted to Edward Brinton and Annie Townsend who undertook the rearing study of *E. gibboides* aboard RV *Alexander Agassiz* during Leg I of Scripps Institution of Oceanography Expedition Krill, May-June 1974.

Reviews of the literature dealing with the larval development of the Euphausiacea and discussions of their larval phases are given by Mauchline and Fisher (1969) and Gopalakrishnan (1973). The nomenclature used in the description of *E. gibboides* is modified from Sars (1885) as follows.

Nauplius phase (two stages): Body oval, unsegmented, without compound eyes; 3 pairs of limbs present, antennulae uniramous, antennae and mandibles biramous and natatory.

Metanauplius phase (one stage): Body unsegmented, with carapace; only 2 pairs of limbs present (antennulae and antennae); mandibles, maxillules, maxillae, and maxillipeds (first thoracic legs) present as bud-like prominences.

Calyptopis phase (three stages): Body divided into two principal sections; abdomen becomes segmented; thoracic segments develop but are much compressed; compound eyes imperfectly developed, immobile and covered by hood-like expansion of carapace; mandibles, maxillae, and maxillipeds distinct and functional; thoracic legs posterior to first leg and pleopods not present; uropods develop.

Furcilia phase (variable number of stages): Compound eyes more fully developed, mobile, and projecting beyond sides of carapace; antennae at first retaining original natatory structure, later transformed to adult form with scale and developing flagellum; legs and pleopods develop; method of locomotion thus changes as setose pleopods replace modified antennae for swimming; photophores develop; terminal telson spines become reduced in number, last furcilia stage with 1 terminal telson spine and 3 posterolateral spines.

Juvenile phase: Begins when telson has 2 posterolateral and 1 terminal telson spines, the adult number.

Individuals were straightened on a glass slide in a drop of preservative for measurement with an ocular micrometer. Measurements of developmental phases were as follows.

Egg: Diameter of capsule and width of perivitelline space measured only in specimens with undeveloped embryos.

Nauplius: Length between midpoints of anterior and posterior margins; width at widest point.

Metanauplius: Length between midpoints of anterior margin of rostral hood and posterior margin of abdomen; width of rostral hood at widest point; width of body at widest point posterior to rostral hood; measurements exclude spinose fringe on rostral hood and telson spines.

Calyptopis: Total length between midpoints of anterior margin of carapace and posterior margin of telson; carapace length from center of anterior margin to distal point on posterior margin excluding dorsal spine; carapace width at widest point on anterolateral margins; measurements exclude spinose fringe of carapace and telson spines.

Furcilia: Total length between midpoints of anterior margin of carapace and posterior margin of telson, the carapace measurement excludes spines until median spine appears and then is made from tip of spine, the telson measurement excludes spines until development of 1 terminal spine in last stage and then is taken from tip of spine; carapace length from posterior margin of orbit to distal point on posterior margin excluding spine in furcilia I; rostrum width at widest point proximal to eyestalks, excluding spines; eye height on cornea between upper and lower lobes measured in lateral view.

Juvenile: Total length as in last furcilia stage.

The range, mean ($\bar{x}$), and standard deviation (SD) of each measurement with number of specimens measured (n) is given in Tables 5-8.

Larvae were placed in glycerine for dissection. The description of setation and form of appendages is based on dissection of at least 10 specimens of each developmental stage. The common form of each appendage is figured; when the setation varies within a stage, the number of appendages with each setation observed is given in parentheses behind the number of setae. Only changes in setation or structure from the preceding stage are noted. Drawings were prepared with a Wild M-20 microscope[2] equipped with drawing attachment.

RESULTS

Developmental Stages

The following larval forms of *E. gibboides* were found: nauplius phase, stages I, II; metanauplius phase, one stage; calyptopis phase, stages I-III; furcilia phase, stages I-VI. There was no variation in the number of stages in nauplius, metanauplius, and calyptopis phases or in the first half of the furcilia phase in which stages are defined by the pattern of pleopod development. In the later furcilia stages, usually characterized by the sequential reduction in number of terminal telson spines, dominant and variant forms were found. The features used to differentiate furcilia in the initial sorting were: number and position of setose and non-setose pleopods, form of antenna, number of terminal telson spines, total length, and relative abundance. The furcilia identified are listed in Table 2.

When representatives of each stage were dissected and studied in more detail, two forms of the furcilia with 3 terminal telson spines were found; one was the dominant furcilia V and the other an advanced form which was comparable in size and development to the furcilia with 1 terminal telson spine. There also were two forms of furcilia with 2 terminal telson spines; the smallest was equivalent to furcilia V and the largest to furcilia VI. The relatively large furcilia with 2 and 3 telson spines considered to be variants of furcilia VI lacked the 2nd (middle) pair of posterolateral spines on the telson of the next instar developing beneath the cuticle and presumably would be classified as juvenile after the

TABLE 2.—The furcilia identified during initial survey.

Stage		Form of antenna	Pairs of pleopods		No. terminal telson spines
			Non-setose	Setose	
I		natatory	1	0	7
II		natatory	3	1	7
III		natatory	1	4	7
IV	dominant	natatory	0	5	5
	variant	natatory	0	5	7
	variant	natatory	0	5	6
	variant	natatory	0	5	4
V	dominant	juvenile	0	5	3
	variant	juvenile	0	5	5
	variant	juvenile	0	5	4
	variant	juvenile	0	5	2
VI		juvenile	0	5	1

TABLE 3.—Some of the characters used to group variant forms of furcilia stages IV-VI.

Character	Stage IV	Stage V	Stage VI
No. terminal telson spines: Dominant	5	3	1
Variant	7, 6, 4	5, 4, 2	3, 2
Antenna: Form	natatory	juvenile	juvenile
Right mandible: Dentate process near incisor teeth	+	+	–
Maxillule: Pseudexopod bud	–	–	+
Pleopod 5: Endopod setae	1	2	4

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

next molt. A few of the details which helped to clarify the relationship between furcilia with variant forms are noted in Table 3.

The total number of dominant and variant forms of furcilia IV-VI in samples examined and the percentage of each form within these stages is given in Table 4. The potential variation in reduction of the number of terminal telson spines was estimated by counting the number of spines developing on the telson of the next instar when possible. The range observed in each form is shown in Table 4.

John (1936) in describing larvae of species of *Euphausia* from the Southern Ocean noted that the "furcilia stages recognized by the number of terminal spines on the telson are not such natural groups as those recognized by the character and number of the pleopods"; this appears to be true as well for *E. gibboides*. As observed in other species (Mauchline and Fisher 1969), there is a general correlation between size of furcilia and the number of terminal telson spines (Tables 7, 8). As the larvae become larger, on the average, the number of spines usually decreases, and stages may be characterized by size, number of spines, and relative abundance. Furcilia identified by a wider range of developmental details, however, seem to be grouped more naturally.

Description of Stages

Nauplius I (Figure 1A)

Body egg-shaped, with 3 pairs of appendages. Antennule (Figure 6A) uniramous, unsegmented, with 1 seta and 2 small spines terminally, and 1 small subterminal spine.

Antenna (Figure 7A) biramous, unsegmented; exopod with 4 setae and tiny tooth distally; endopod with 2 setae and small spine terminally and 1 subterminal seta.

Mandible (Figure 7G) biramous, unsegmented; endopod and exopod each with 3 setae.

TABLE 4.—The number of dominant and variant forms of furcilia IV, V, and VI observed, the percentage of each form within stage, and the variation in number of terminal telson spines on developing telson of next instar among individuals of each form.

Stage	No. terminal telson spines	No. larvae	% of stage	No. terminal telson spines in next instar
IV dominant	5	242	88.6	5, 4, 3, or 2
variant	7	9	3.3	5
variant	6	17	6.2	5, 4, or 3
variant	4	5	1.8	3 or 2
V dominant	3	122	78.7	3 or 1
variant	5	11	7.1	3
variant	4	14	9.0	3, 2, or 1
variant	2	8	5.2	1
VI dominant	1	76	66.1	1
variant	3	21	17.8	1
variant	2	19	16.1	1

Nauplius II (Figure 1B)

Body longer, with 2 pairs posterior spines, outer pair very small.

Antennule (Figure 6B) with 2 setae and 1 spine terminally, and a small subterminal spine.

Antenna (Figure 7B) with 5 setae and sometimes a rudimentary 6th seta on exopod. Endopod with 3 setae and a small spine terminally, and 1 subterminal seta.

Mandible as in nauplius I.

Metanauplius (Figure 1C, D)

Carapace produced into wide rostral hood fringed with marginal spines; anterior margin with 3 or 4 relatively long pairs interspersed; posterolateral lobes curved ventrally around body; dorsal crest prominent, without spines. Abdomen short, posterior margin with median indentation and 5 pairs of spines; 3rd pair relatively long bearing setules, other pairs small and fused with telson, one or both of inner pair sometimes rudimentary. There are only 2 pairs of functional appendages.

Antennule (Figure 6C) with 2 setae, 1 aesthetasc (sensory seta), and 1 spine terminally and a small subterminal spine.

Antennal exopod and endopod (Figure 7C) articulated with basal segment which may show incipient segmentation. Exopod with 6 setae on 5 small distal segments; terminal segment, too small to be visible in figure, bears 2 setae. Endopod with 4 setae and 2 small spines distally and 1 subterminal seta on inner margin; rudiment of proximal 2nd marginal seta sometimes present.

Mandibles, maxillules, maxillae, and maxillipeds present as rudimentary buds.

Calyptopis I (Figure 2A-C)

Carapace with distinctive broad rostral hood fringed with small marginal spines; lateral

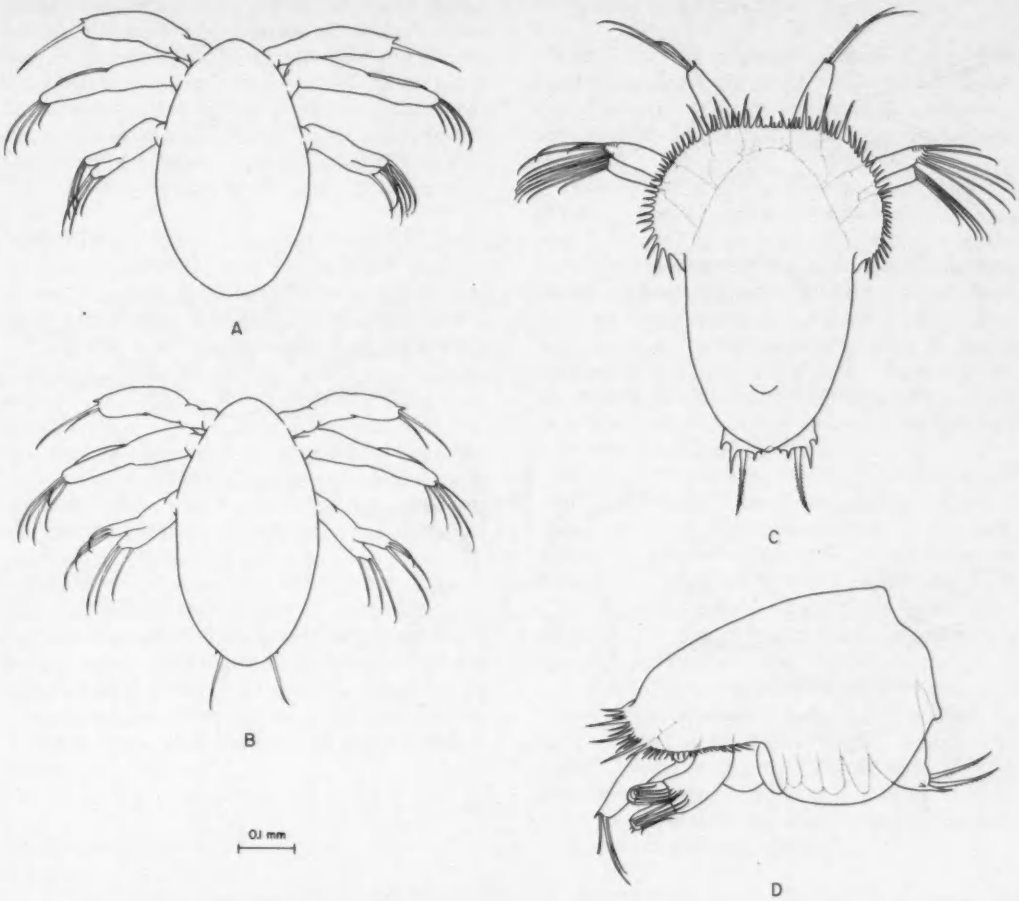

FIGURE 1.—Nauplius I: A, dorsal view. Nauplius II: B, dorsal view. Metanauplius: C, dorsal view; D, lateral view.

margins constricted behind eyes; posterior margin produced into strong dorsal spine; dorsal crest prominent. Compound eyes widen as they develop during stage, striated body of photophore visible. Thoracic segments may be visible; abdomen unsegmented.

Antennule (Figure 6D) 2-segmented, basal segment with 2 dorsal setae, 1 medial seta, and medial spine on distal margin; small terminal segment with 2 aesthetascs, 3 setae, 1 strong medial spine and tiny spine.

Antenna (Figure 7D) with 2-segmented protopod. Exopod with 7 setae on 5 distal segments; terminal segment with 3 setae, subterminal segments with 1 seta each. Endopod with 4 terminal setae and 2 setae on inner margin, the proximal marginal seta may be rudimentary; in addition to setules, distal marginal seta and 2 terminal setae bear small spinules and 3rd terminal seta armed with proximal row of comblike setules. This setation remains unchanged until furcilia V.

Mandibles (Figure 7H) asymmetrical; both with narrow plate near *pars molaris* and tuft of setae at base of plate; right mandible with dentate process near incisor teeth; when mandibles close dentate process bends inward toward mouth, the lower plates overlap. Conical anterolateral process and small prominent lateral knob present; lateral knob disappears in furcilia I, and anterolateral process decreases in size gradually up to late furcilia stages.

Maxillule (Figure 8A) with 6(1) or 7(20) setae

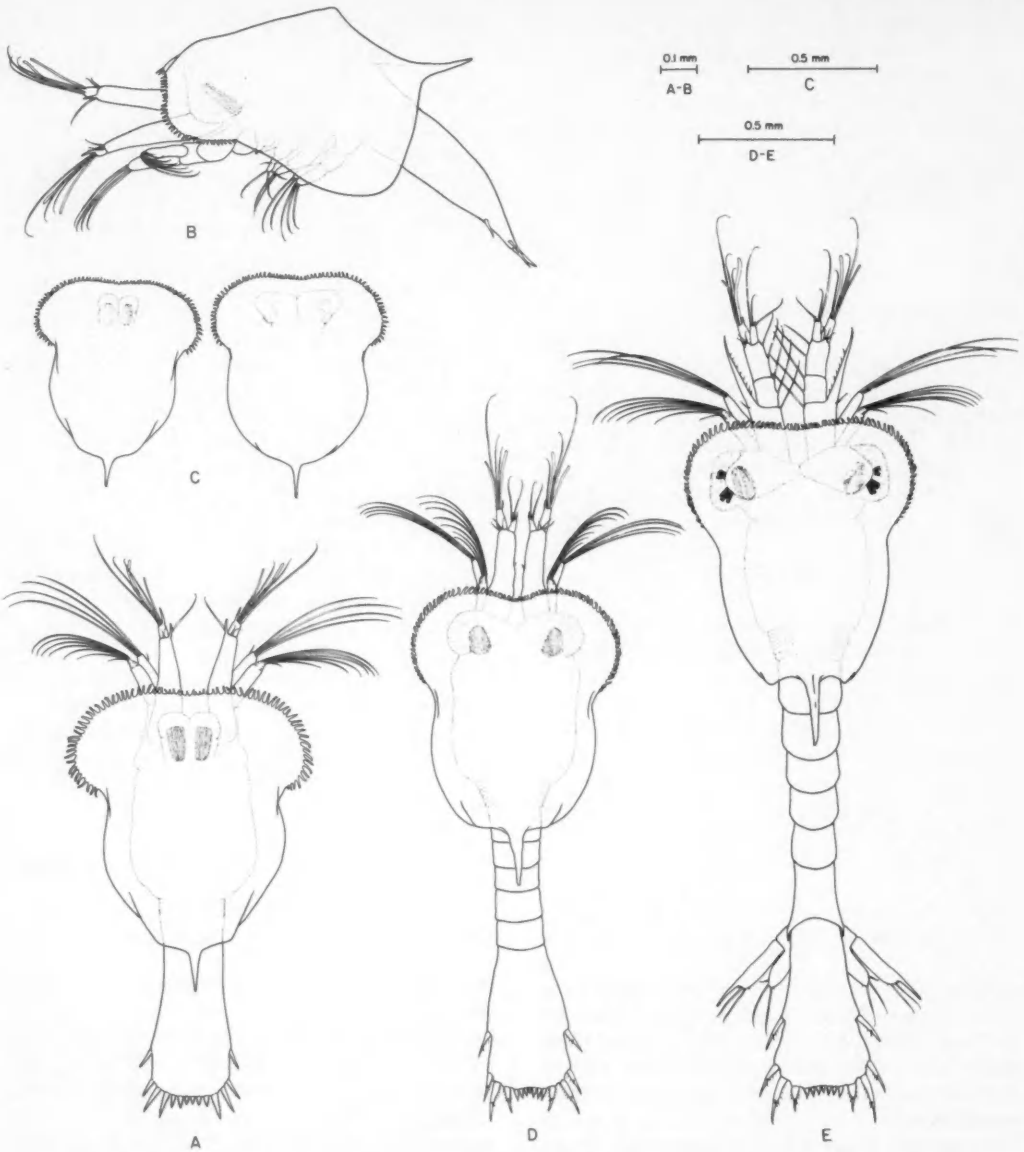

FIGURE 2.—Calyptopis I: A, dorsal view; B, lateral view; C, development of eyes within stage. Calyptopis II: D, dorsal view. Calyptopis III: E, dorsal view.

on coxal endite, 1 of 2 large setae distinctively armed distally with strong triangular spines rather than setules; basal endite with 3 spines armed with spinules. Endopod 2-segmented, terminal segment with 3 and proximal segment with 2 setae. Exopod a small lobe with 4 plumose setae. Setation of endopod does not change until furcilia V and that of exopod does not change throughout larval development.

Maxilla (Figure 8H) with 5 setose lobes on inner

margin (proximal 2 considered coxal and distal 3 basal although segmentation is unclear); setation of medial lobes 1-5 progressing distally is 8-4-4-4-3; 2 setae on lobe 1 and 1 seta on lobes 2-4 situated submarginally on posterior face. Endopod 1-segmented with 3 setae; exopod represented by 1 plumose seta on lateral margin. There is no change in setation in calyptopis phase.

Maxilliped (Figure 9A) usually with 5 setae on coxa, 4 marginal and 1 (sometimes absent) on posterior face, 4(3) or 5(17) setae were observed. Basis with 6 setae. Endopod 2-segmented; terminal segment with 4 and proximal segment with 3 setae; 1 distal seta on basis and 1 on proximal segment of endopod situated submarginally on posterior face; 1 marginal seta on basis and 1 on first segment of endopod relatively short and stout with tiny marginal spinules. Exopod with 4 terminal setae and 1 proximal seta near indistinct articulation with basis. Fine marginal hairs present as figured.

Telson with 1 pair of lateral spines, 3 pairs of posterolateral spines and 6 terminal spines, posterolateral spine 3 (inner) slightly longer than central posterolateral spine 2; terminal spines and posterolateral spine 3 armed with spinules on lateral margins, lateral spines and posterolateral spines 1 and 2 with spinules on inner margins only.

Calyptopis II (Figure 2D)

Broad rostral hood of carapace with more pronounced inward curve between eyes; dorsal crest less prominent. Abdomen with 5 segments.

Antennule (Figure 6E) biramous. Peduncle unsegmented but may be constricted with segmentation of calyptopis III visible beneath cuticle; distal margin with 3 dorsal setae and inner margin with 1 seta. Outer ramus with 2 aesthetascs, 1-3 setae and 2-4 spines terminally; inner ramus short, with 2 setae and 1-4 spines.

Maxillule (Figure 8B) with 6(3) or 7(15) setae on coxal endite; basal endite with 5 spines.

Maxilliped with 4(1) or 5(19) setae on coxa.

Telson, with addition of small median spine, armed with 7 terminal spines; posterolateral spine 2 now longest; lateral and posterolateral spines with relatively large dorsal spinule slightly more than halfway to tip.

Calyptopis III (Figure 2E)

Carapace with rudiment of small denticle on posterolateral margin present in furcilia I (Figure 4A). Abdomen with 6 segments; 6th segment, now separate from telson, with pair of biramous uropods.

Antennule (Figure 6F) with 3-segmented peduncle, basal segment produced distally into strong lateral spine extending to or slightly beyond tip of inner ramus, inner margin of spine setose. Peduncle segments 1-3 with 1-2-2 plumose setae on inner margins; segment 3 with dorsal lobe bearing 3 setae on distal margin; basal segment with 1 large lateral seta at base of spine. Inner flagellum about two-thirds length of outer flagellum and may have 3rd terminal seta; otherwise setation of rami unchanged.

Mandible armature (Figure 7I) unchanged.

Maxillule with 7 setae on coxal endite and 5 spines on basal endite; no variation observed.

Maxilla usually unchanged, with setation of 8-4-4-4-3 on lobes 1-5; lobe 3 varied with 3(1) or 4(20) setae and lobe 5 with 2(1) or 3(20) setae.

Maxilliped (Figure 9B) usually with 6 setae on coxa, 5(3) or 6(16) setae were observed.

Uropod (Figure 11Q) biramous; protopod with ventral spine above endopod; exopod with strong posterolateral spine, 2 small spines and 2 setae distally; endopod incompletely articulated with protopod, bearing 1 spine and 2 setae distally and 1 small subterminal dorsally projecting seta.

Telson armature unchanged.

Furcilia I (Figures 3A, 4A)

Eyes large, stalked and moveable, with 3-lobed appearance due to arrangement of ommatidia and concentrations of pigment as well as constrictions in cornea; lower lobe largest and most distinctly defined; convex middle lobe especially contributes to characteristic shape of eye. Carapace emarginate behind eyes; rostrum broad, blunt, fringed with small spines; posterior margin produced into dorsal spine; posterolateral margins with denticle; dorsal crest near midlength. First segment of abdomen with pair of non-setose pleopods; developing photophore between pleopods sometimes with faint pigment. Small anal spine present.

Antennule (Figure 6G) with lateral spine of peduncle segment 1 extending to distal margin

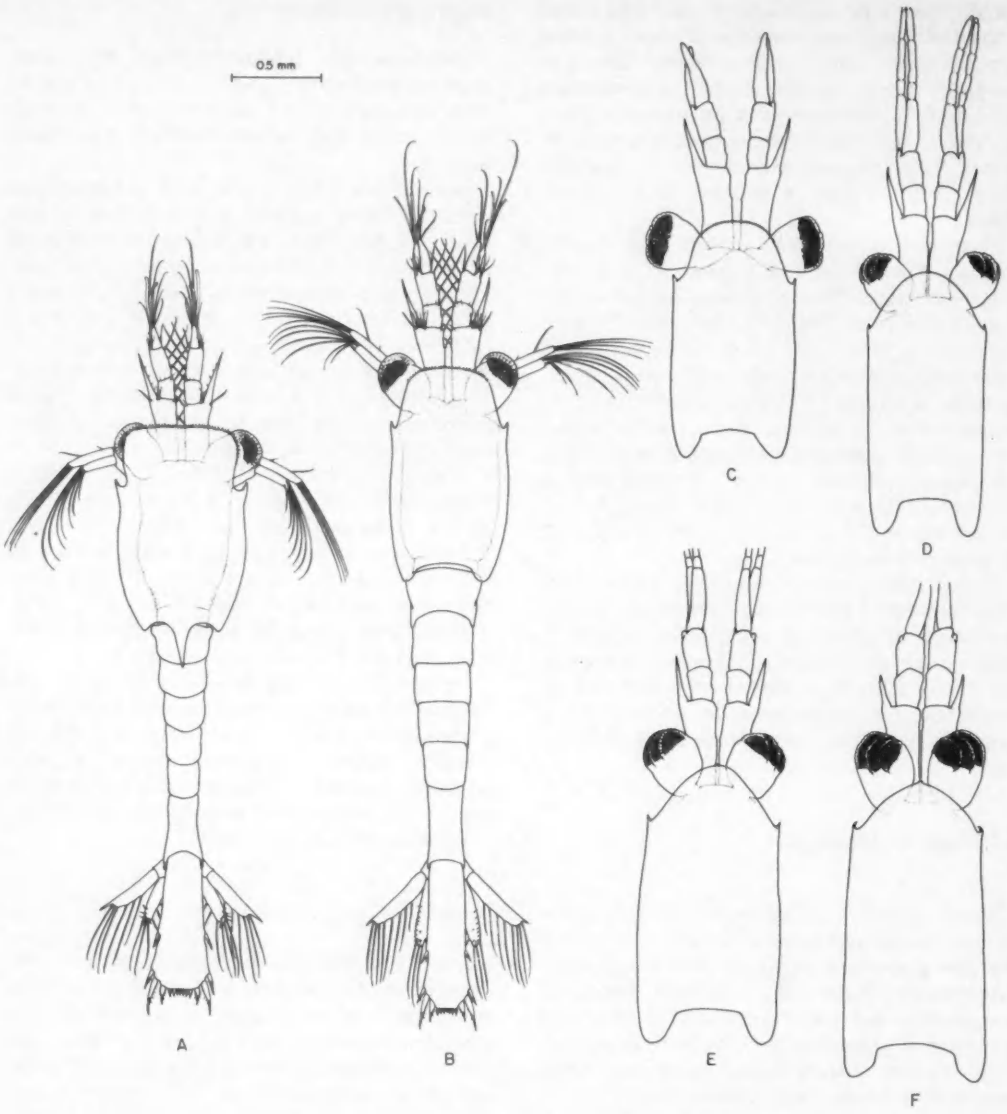

FIGURE 3.—Dorsal view: A, furcilia I; B, furcilia II; C, furcilia III; D, furcilia IV; E, furcilia V; F, furcilia VI.

of segment 3; spine with 5 pairs of setae spaced along inner margin and small setae between; peduncle segments 1 and 2 each with 2 plumose setae on inner margin and small dorsal setae; segment 3 with 3 setae on inner margin, a 4th slightly ventral seta on distal margin, and 4 setae on dorsal lobe. Flagella usually of equal length; outer ramus with 1 aesthetasc at about midlength of inner margin; terminal setation of flagella apparently unchanged but too frequently broken to determine. In subsequent furciliar stages numbers of setae on dorsal surface increase but

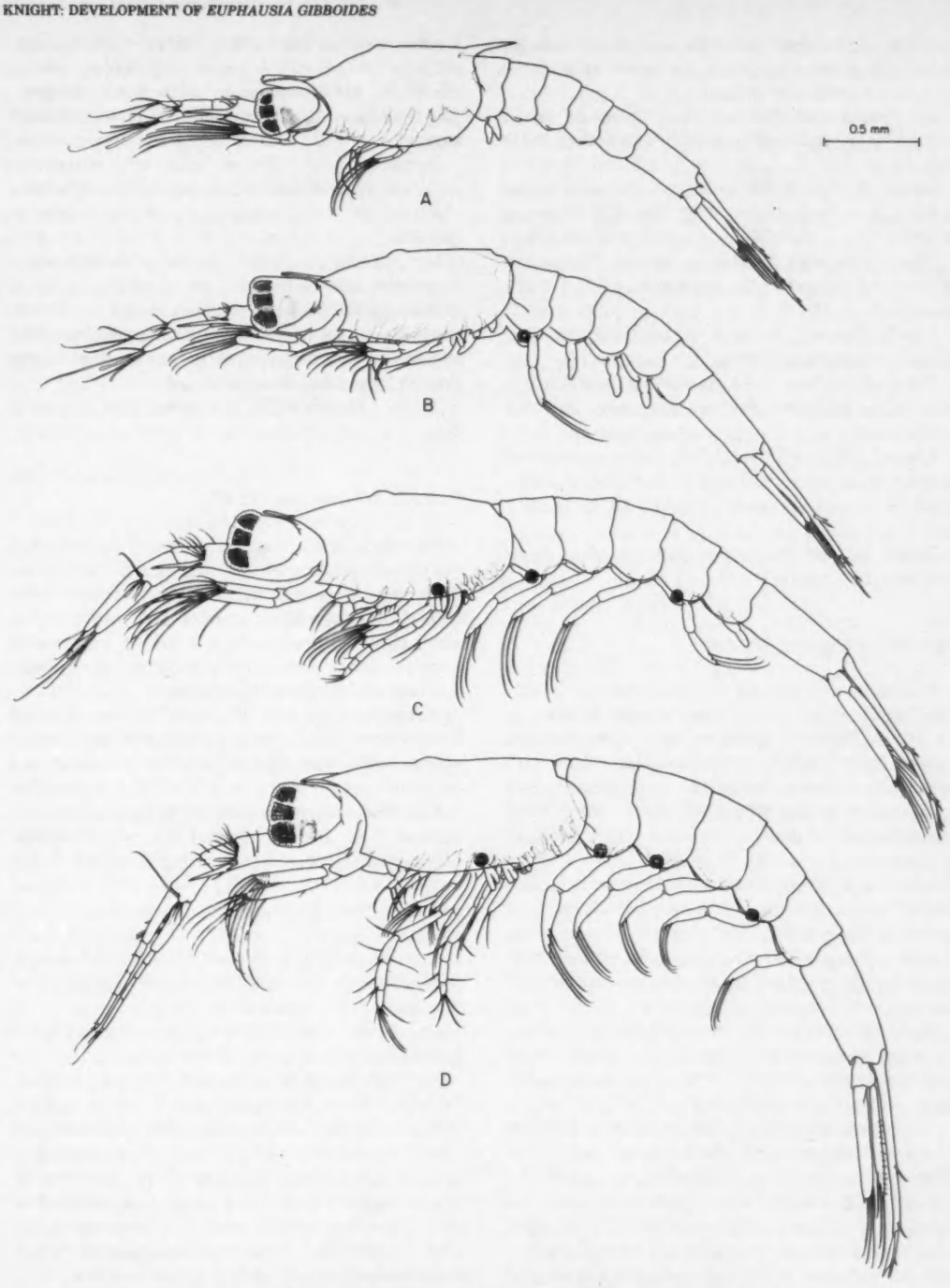

FIGURE 4.—Lateral view: A, furcilia I; B, furcilia II; C, furcilia III; D, furcilia IV.

number of plumose setae on medial margin remain the same; the lateral spine on segment 1 gradually decreases in length.

Maxillule with 6(2) or 7(20) setae on coxal endite; basal endite (Figure 8C) with 6(1) or 7(21) spines.

Maxilla (Figure 8I) usually with setation of 8-4-5-4-3 on inner lobes 1-5; lobe 3 now bears 5 setae; lobe 1 variable, with 7(1) or 8(20) setae.

Maxilliped with 5 setae on terminal segment of endopod (Figure 9C); coxa with 5(3) or 6(18) setae.

Leg 2 (Figure 10A) present, rudimentary; bud of leg 3 sometimes visible.

Pleopod (Figure 11L) non-setose and unsegmented, or with incipient segmentation and bud of endopod.

Uropod (Figure 11R) with 6 plumose setae on exopod; endopod articulated with protopod, bearing 6 marginal plumose setae and 3-5 small dorsal setae.

Telson (Figure 12A) with posterolateral spine 2 relatively longer.

Furcilia II (Figures 3B, 4B)

Rostrum of carapace a little narrower, with smaller marginal spines; posterior margin without dorsal spine; lobes of eye more defined (Figure 6K). Abdomen with 1 pair setose and 3 pairs non-setose pleopods on segments 1-4 respectively; photophore on segment 1 pigmented and functional, developing photophore on segment 4 sometimes with faint pigment.

Antennule (Figure 6H) with 5 setae on dorsal lobe of peduncle segment 3 one of which projects dorsally; this setation, with dorsally oriented seta becoming longer and stronger, is found in subsequent furcilia stages. Flagella now approximately as long as 3rd segment of peduncle.

Maxillule (Figure 8D) with 7(1) or 8(23) setae on coxal endite; basal endite with 7 marginal spines and often, in 16 of 24 appendages, with small seta on proximal margin.

Maxilla usually with setation of 8-4-5-5-3; lobe 3 variable with 5(23) or 6(1) setae and lobe 4 (Figure 8J) with 4(3) or 5(21) setae.

Maxilliped usually with 6 setae on terminal segment of endopod (Figure 9D), 5(3) or 6(21) setae were observed; coxa with 5(1) or 6(23) setae.

Leg 2 (Figure 10B) with endopod bearing 2 terminal setae and unsegmented or with 2 or 3 weakly defined segments; exopod rudimentary, without setae; gill bilobed; developing photophore on coxa sometimes with faint pigment. Leg 3 (Figure 10H) rudimentary, or with bud of exopod and gill. Bud of leg 4 may be present.

Setose pleopod 1 (Figure 11M) with 6 plumose setae on exopod, small endopod with single seta and median hook; non-setose pleopods 2-4 as in furcilia I.

Uropod (Figure 11S) with 8(21) or 9(1) setae on exopod, endopod with 7 marginal and 11 or 12 dorsal setae. This is the last stage in which numbers of setae can be counted; in preserved specimens the marginal setae are too frequently broken to attempt enumeration.

Telson (Figure 12B) narrower, posterolateral spine 3 wider basally.

Furcilia III (Figures 3C, 4C)

Carapace with rostrum narrowing, anterior marginal spines may be very small remnants. Abdomen with 4 pairs setose and 1 pair non-setose pleopods on segments 1-4 respectively; photophores on segments 1 and 4 pigmented and functional; developing photophore on segment 2 sometimes with faint pigment.

Antennular flagella (Figure 6I) almost twice as long as peduncle segment 3 and may be 2-segmented; outer flagellum with 2 aesthetascs on inner margin one of which bifurcates distally.

Mandible with anterolateral process about one-half as long as that figured for calyptopis III.

Maxillule with 8 setae on coxal endite; basal endite (Figure 8E) with 7(1), 8(4), or 9(17) spines on medial margin and 1 small seta on proximal margin.

Maxilla usually with setation of 8-4-6-5-3; lobe 3 (Figure 8K) now with 5(2) or 6(20) setae; lobe 5 variable with 2(1) or 3(20) setae.

Maxilliped with 5(3) or 6(16) setae on coxa and 6 on terminal segment of endopod.

Leg 2 (Figure 10C) with endopod 5-segmented, articulation with basis indistinct, setation variable, terminal segment with more than 2 setae; exopod with 0(7), 1(5), or 2(5) setae; gill bilobed; photophore pigmented and functional. Leg 3 (Figure 10I) with endopod unsegmented or with a few (less than 5) weakly defined segments, setation variable, distal segment usually with 2 terminal setae, 2(21) or 3(1) setae were observed; exopod rudimentary, without setae; gill bilobed.

Leg 4 (Figure 1ON) rudimentary, with bud of exopod and small bilobed or simple bud of gill; endopod usually without terminal setae, 0(22) or 1(2) seta were observed. Leg 5 present as bud. Leg 7 rudimentary with gill bud and developing photophore.

Setation of pleopods on abdominal segments 1-4 as follows: pleopod 1 (Figure 11N) — endopod 2, exopod 6(8), 7(11), or 8(1); pleopods 2-4 — endopod 1, exopod 6. Non-setose pleopod of segment 5 as in furcilia I. Endopod of pleopod 1 with *appendix interna*, a small medial lobe with tiny hooks.

Telson (Figure 12C) narrower; posterolateral spine 3 quite broad, inner margin smooth except for 1 or 2 tiny distal spinules near larger dorsal spinule. Five terminal spines of furcilia IV may often be seen beneath integument.

Furcilia IV (Figures 3D, 4D)

Rostrum of carapace usually with smooth margin, there may be tiny remnants of marginal spines but no median spine. Abdomen with 5 pairs of setose pleopods; photophores on segments 1, 2, and 4 pigmented and functional; developing photophore on segment 3 sometimes with faint pigment.

Antennular flagella (Figure 6J) with about 6 or 7 segments, segmentation usually indistinct; outer flagellum with 3 aesthetascs, 1 proximal to pair on medial margin, 1 aesthetasc no longer bifurcate.

Maxillule with 8(12) or 9(10) setae on coxal endite (Figure 8F); basal endite with 8(1) or 9(21) marginal spines and 1 seta on proximal margin.

Maxilla usually unchanged, with setation of 8-4-6-5-3; lobe 4 variable with 5(20) or 6(2) setae.

Maxilliped (Figure 9E) with 5(4) or 6(18) setae on coxa; basis with 6(9) or 7(10) setae. Endopod becoming 3-segmented as small terminal segment forms with setation of 3-2-4 for segments 1-3.

Leg 2 (Figure 10D) with endopod larger, more setose, and becoming geniculate with terminal 3 segments reflexed as in adult; exopod with 4(3) or 5(6) setae (seldom intact); gill bilobed. Leg 3 (Figure 10J) with endopod 5-segmented, sometimes slightly reflexed, articulation with basis indistinct, setation variable, terminal segment with more than 2 setae; exopod with 2(1), 3(1), or 4(12) setae; gill bilobed. Leg 4 (Figure 10O) endopod with few (less than 5) weakly delineated segments, terminal segment with 2 setae, other setation variable; exopod usually without setae, 1 of 15 appendages examined with 1 seta; gill bilobed. Leg 5 (Figure 11A) rudimentary with bud of exopod and bilobed or simple bud of gill. Bud of leg 6 present. Leg 7 (Figure 11I) with gill bilobed or with small bud of 3rd lobe, photophore may have pigment. Leg 8 (Figure 11F) represented by bilobed or trilobed gill.

Pleopod setation as follows: pleopod 1 (Figure 11O) — endopod 3(2) or 4(17), exopod 8; pleopod 2 — endopod 2, exopod 7(1) or 8(19); pleopod 3 — endopod 2, exopod 7(3) or 8(15); pleopod 4 — endopod 2, exopod 7(8) or 8(9); pleopod 5 — endopod 1, exopod 6.

Telson (Figure 12D) with 5 terminal spines, the 3 terminal spines of next instar often visible beneath cuticle.

VARIANT FORMS. — A small furcilia IV with 6 telson spines was less mature in that leg 4 had 1 terminal seta and exopods of pleopods 3 and 4 had only 6 setae. A furcilia IV with 4 telson spines showed bud of 3rd lobe of gill on leg 2.

Furcilia V (Figures 3E, 5A)

Rostrum usually with smooth margin, there may be a very small median spine. Photophores on abdominal segments 1-4 now pigmented.

Antennule with lateral spine of peduncle segment 1 extending to about midpoint of segment 3, none of the specimens available had flagella intact.

Antenna (Figure 7E) transformed, no longer natatory; basal segment with distolateral spine; endopod with 8 segments, 3 peduncular and 5 flagellar, division of terminal segment not always distinct; exopod (scale) with 13 or 14 plumose marginal setae.

Mandible (Figure 7J) with anterolateral process now considerably reduced in size.

Maxillule with 8(1) or 9(22) setae on coxal endite; basal endite with 9(21) or 10(2) marginal spines and 1(21) or 2(2) small setae on proximal margin. Endopod with segmentation weak or indistinct; in 6 of 21 appendages examined 1-segmented with 1 seta on lateral margin as figured for furcilia VI (Figure 8G).

Maxilla usually with setation of 8-4/5-6-6-3; lobe 2 (Figure 8L) variable with 4(15) or 5(9) setae and lobe 4 with 4(1), 5(4), or 6(19) setae.

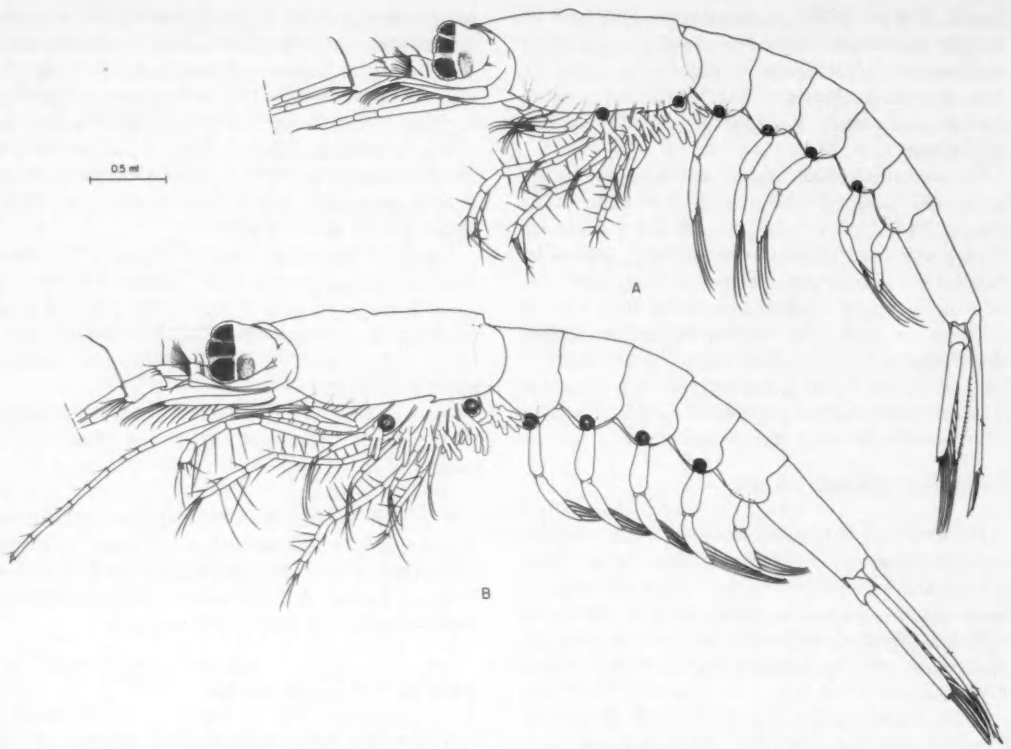

FIGURE 5.—Lateral view: A, furcilia V; B, furcilia VI.

Maxilliped (Figure 9F) with increasingly variable setation; coxa with 5(2), 6(12), 7(9), or 8(1) setae; basis with 6(2), 7(9), or 8(12) setae. Endopod lengthened, usually with 3 segments; 4 of 20 appendages examined with 4 or 5 segments indicated, distal segments weakly delineated; setations of 3-2-4, 3-1-1-4, and 3-2-0-1-4, progressing distally, were observed.

Leg 2 (Figure 10E) with dactyl of endopod becoming modified; exopod with 6 setae; gill usually with bud of 3rd lobe. Leg 3 (Figure 10K) with endopod reflexed, longer and more setose; exopod with 5(8) or 6(8) setae; gill with bud or sizeable rudiment of 3rd lobe. Leg 4 (Figure 10P) with endopod 5-segmented, articulation with basis never clear, setation variable, terminal segment with more than 2 setae; exopod with 4(16) or 5(1) setae; gill bilobed. Leg 5 (Figure 11B) with endopod unsegmented or weakly segmented with less than 5 segments, with 1(9) or 2(13) terminal setae and sometimes a few marginal setae; exopod with 0(22) or 1(1) seta; gill bilobed. Leg 6 (Figure 11D) rudimentary with gill bud, may be slightly bifid. Leg 7 (Figure 11J) with pigmented photophore; gill sometimes with bud of 3rd or 4th lobes. Leg 8 (Figure 11G) ramified, with varying numbers of lobes.

Setation of pleopods as follows: pleopod 1 — endopod 4, exopod 8(11), 9(5), or 10(2); pleopod 2 — endopod 4, exopod 8(7), 9(11), or 10(1); pleopod 3 — endopod 4, exopod 8(15) or 9(5); pleopod 4 — endopod 3(1) or 4(19), exopod 8; pleopod 5 — endopod 2, exopod 6(1), 7(17), or 8(5).

Telson (Figure 12E) narrow, with 3 terminal spines, 3rd pair of posterolateral spines lengthening relatively; single terminal spine of final furcilia may often be seen beneath cuticle.

VARIANT FORM. — A small furcilia V with 5 telson spines had antennal flagellum of about 5 segments, endopod of leg 5 without terminal setae, and endopod of pleopods 3-5 with 2, 2, and

1 setae respectively, one of the endopods of pleopod 5 had rudiment of 2nd seta.

Furcilia VI (Figures 3F, 5B)

Rostrum usually with small median spine.

Antennule with lateral spine of peduncle segment 1 about as long as segment 2; outer flagellum may have additional proximal aesthetasc; one apparently intact inner flagellum with 10 segments.

Antennal scale (Figure 7F) with approximately 15 or 16 setae; one intact flagellum with 3 peduncular and 11 flagellar segments.

Right mandible (Figure 7K) now without dentate process near incisor teeth; toothed plates relatively smaller; rudimentary palp may begin to increase in size.

Maxillule (Figure 8G) with 9(15) or 10(9) setae on coxal endite; basal endite with 9(4) or 10(20) marginal spines and 1(8) or 2(16) small setae on proximal margin. Endopod of 1 segment with 1 proximal lateral seta; terminal and medial setation unchanged. Coxa now with rudiment of pseudexopod.

Maxilla (Figure 8M) usually with setation of 8-6-6-6-3; lobe 2 variable with 4(2), 5(4), or 6(18) setae. Exopod represented by 1 (22) or 2(2) setae; endopod rounder.

Maxilliped (Figure 9G) modifying to adult form; coxa with 5-9 setae, long seta on posterior face no longer present; basis with 8(22) or 9(2) setae. Endopod of 5 segments with variable setation; articulation with basis not clear. Exopod still with 4 terminal setae.

Leg 2 (Figure 10F, G) with endopod more setose, dactyl with a few more "cleaning" comb setae; exopod with 6 setae; gill trilobed. Leg 3 (Figure 10L, M) with long terminal setae on dactyl of endopod; exopod with 6 setae; gill with bud of 3rd lobe or trilobed. Leg 4 (Figure 10Q) with endopod reflexed; exopod with 5(1) or 6(14) setae; gill with bud or larger rudiment of 3rd lobe. Leg 5 (Figure 11C) with endopod 5-segmented and setation variable, terminal segment with more than 2 setae; exopod with 1(2), 2(4), 3(2), or 4(10) setae; gill trilobed. Leg 6 (Figure 11E) with endopod unsegmented and nonsetose; exopod without setae; gill trilobed; exopod and gill may be rudimentary. Legs 7 (Figure 11K) and 8 (Figure 11H) with increasing number of gill lobes.

Pleopods with setation as follows: pleopod 1 (Figure 11P) — endopod 4(5), 5(10), or 6(7), exopod 9(7) or 10(12); pleopod 2 — endopod 4(14), 5(7), or 6(2), exopod 9(2), 10(13), or 11(3); pleopod 3 — endopod 4(17), 5(1), or 6(3), exopod 9(2), 10(13), or 11(1); pleopod 4 — endopod 4(21) or 6(2), exopod 9(10) or 10(7); pleopod 5 — endopod 3(1) or 4(20), exopod 8.

Telson (Figure 12F) quite slender with 1 terminal spine and 3 pairs posterolateral spines; posterolateral spine 2 was missing on one side in 5 of 12 larvae dissected. Developing telson of next instar is without spine 2 on either side.

VARIANT FORMS. — In furcilia VI with 2 and 3 telson spines, basis of maxilliped sometimes with 7 setae and exopod of leg 2 with 6, 7, or 8 setae. Once in furcilia with 3 telson spines, lobe 3 of maxilla with 7 setae and right mandible with tiny remnant of dentate process.

Measurements

The eggs assumed to be those of *E. gibboides* have a relatively wide perivitelline space. The measurements, in millimeters, of 100 eggs from one sample (6304-110.70) are: diameter of capsule, range = 0.61-0.75, $\bar{x}$ = 0.69, SD = 0.03; perivitelline space, range = 0.13-0.19, $\bar{x}$ = 0.16, SD = 0.01.

The measurements of developmental stages are given in Tables 5-8. The growth factor (mean length in stage divided by mean length in preceding stage) for dominant forms is as follows:

Stage	*Growth factor*	*Stage*	*Growth factor*
		Furcilia I	1.23
Nauplius II	1.04	Furcilia II	1.17
Metanauplius	1.08	Furcilia III	1.14
Calyptopis I	2.03	Furcilia IV	1.10
Calyptopis II	1.55	Furcilia V	1.10
Calyptopis III	1.39	Furcilia VI	1.12

There was variation in size of comparable developmental stages between the different areas from which samples were studied. The lengths of calyptopis stages are compared in Table 9. The larvae sampled in April 1963 (Cruise 6304) in the eastern North Pacific became larger, on the average, during the calyptopis phase in the

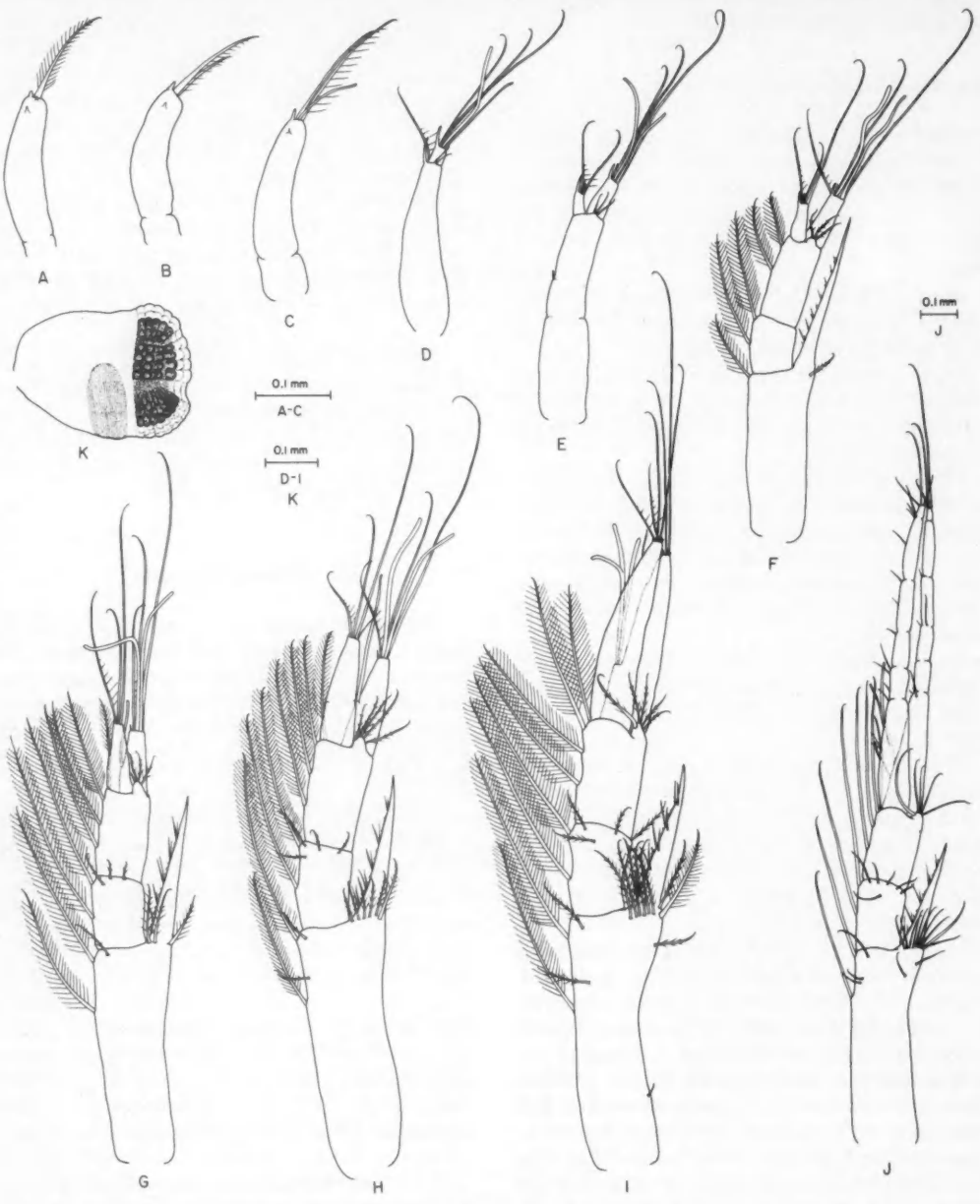

FIGURE 6.—Antennule: A, nauplius I; B, nauplius II; C, metanauplius; D, calyptopis I; E, calyptopis II; F, calyptopis III; G, furcilia I; H, furcilia II; I, furcilia III; J, furcilia IV. Eye: K, furcilia II.

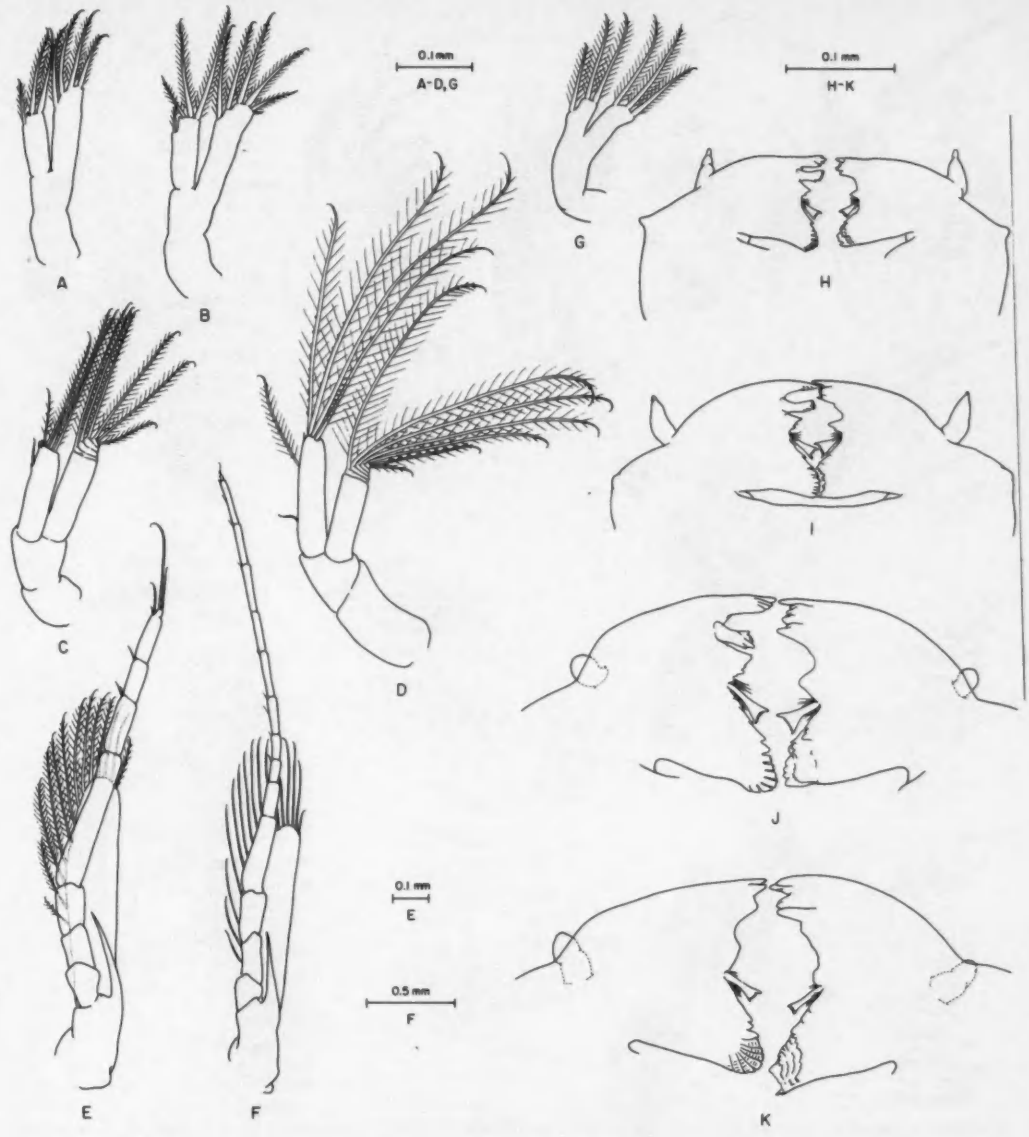

FIGURE 7.—Antenna: A, nauplius I; B, nauplius II; C, metanauplius; D, calyptopis I; E, furcilia V; F, furcilia VI. Mandibles: G, nauplius I; H, calyptopis I; I, calyptopis III; J, furcilia V; K, furcilia VI.

FIGURE 8.—Maxillule: A, calyptopis I; B, calyptopis II; C, furcilia I, basal endite; D, furcilia II; E, furcilia III, basal endite; F, furcilia IV, coxal endite; G, furcilia VI. Maxilla: H, calyptopis I; I, furcilia I; J, furcilia II, lobe 4; K, furcilia III, lobe 3; L, furcilia V, lobe 2; M, furcilia VI.

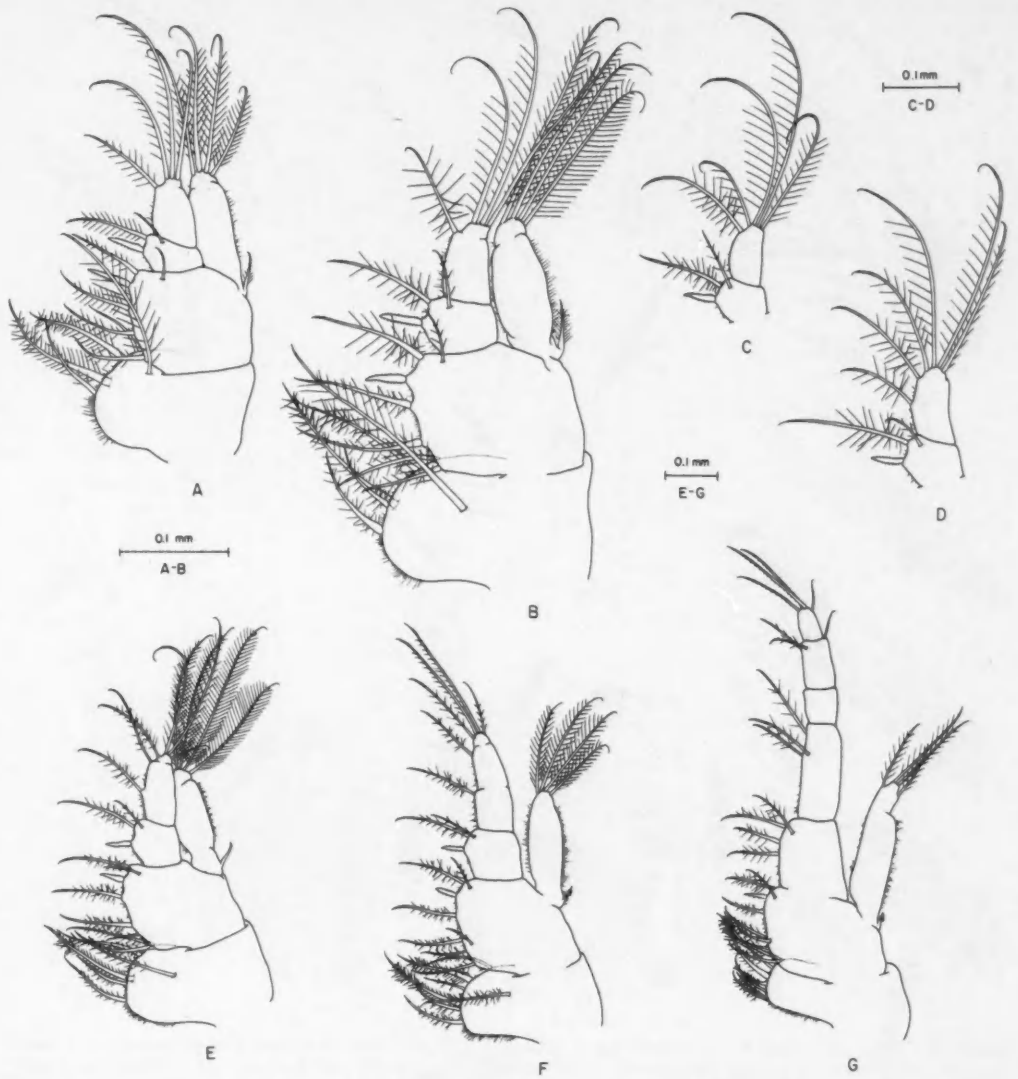

FIGURE 9.—Maxilliped (leg 1): **A**, calyptopis I; **B**, calyptopis III; **C**, furcilia I, endopod; **D**, furcilia II, endopod; **E**, furcilia IV; **F**, furcilia V; **G**, furcilia VI.

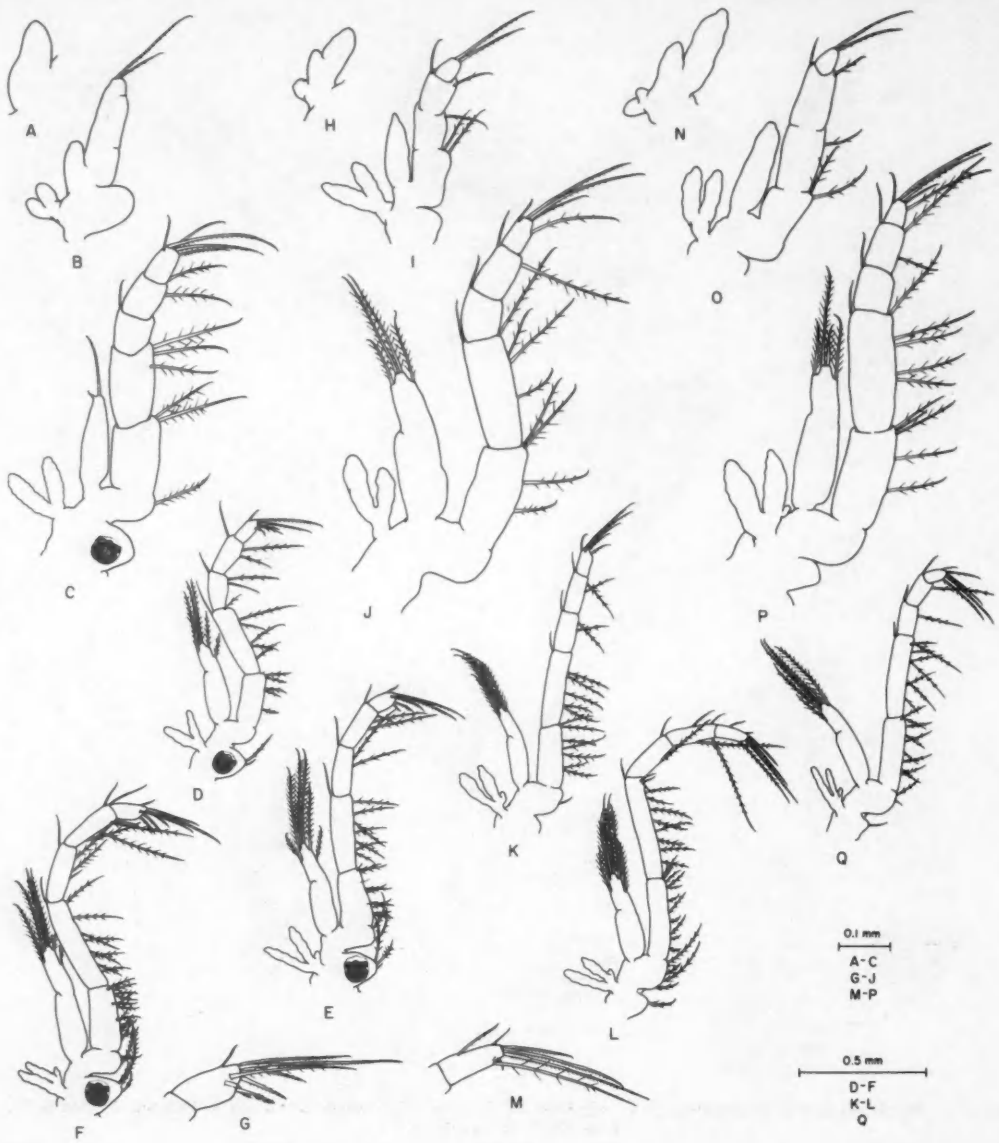

FIGURE 10.—Thoracic legs. Leg 2: A, furcilia I; B, furcilia II; C, furcilia III; D, furcilia IV; E, furcilia V; F, furcilia VI; G, dactyl, furcilia VI. Leg 3: H, furcilia II; I, furcilia III; J, furcilia IV; K, furcilia V; L, furcilia VI; M, dactyl, furcilia VI. Leg 4: N, furcilia III; O, furcilia IV; P, furcilia V; Q, furcilia VI.

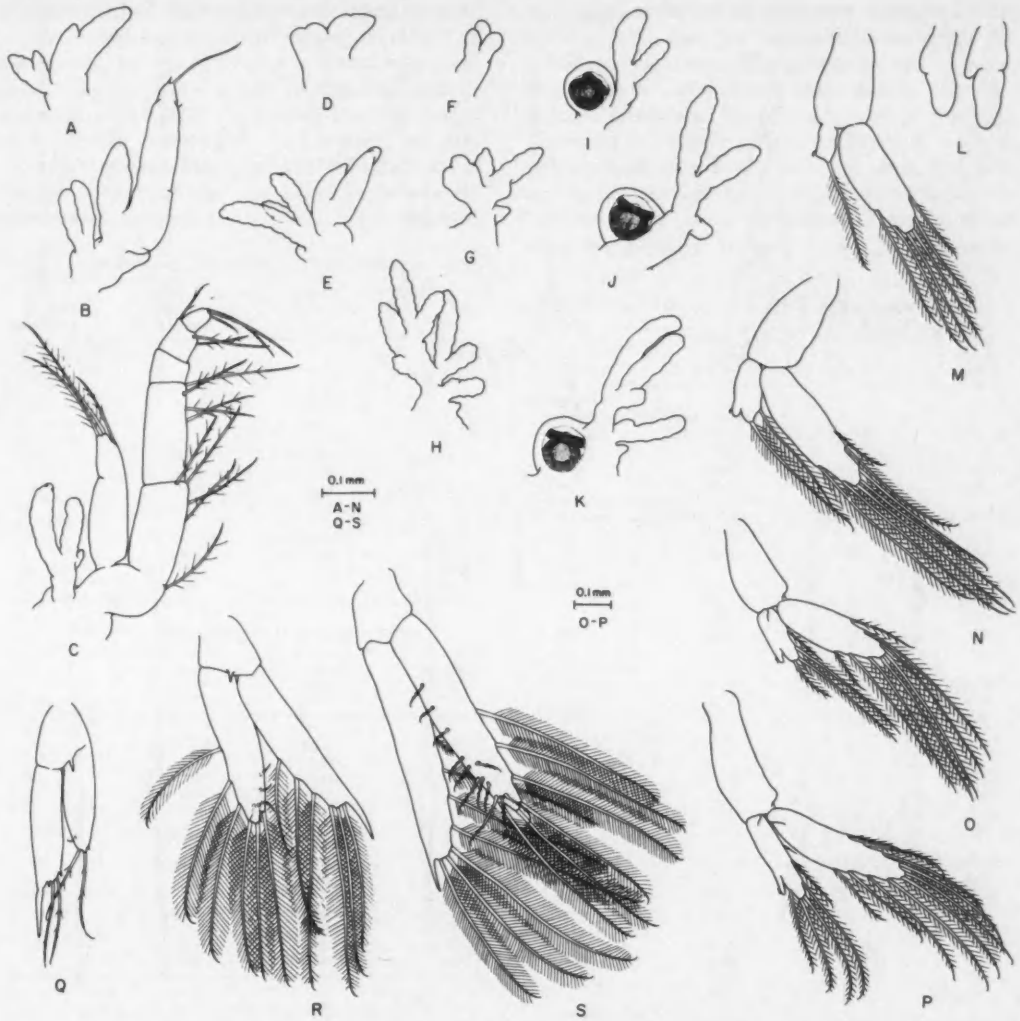

FIGURE 11.—Thoracic leg 5: A, furcilia IV; B, furcilia V; C, furcilia VI. Leg 6: D, furcilia V; E, furcilia VI. Leg 7: I, furcilia IV; J, furcilia V; K, furcilia VI. Leg 8: F, furcilia IV; G, furcilia V; H, furcilia VI. Pleopod 1: L, furcilia I; M, furcilia II; N, furcilia III; O, furcilia IV; P, furcilia VI. Uropods: Q, calyptopis III; R, furcilia I; S, furcilia II.

more northern areas. In the sample from August 1963 (6306-117.80), the sizes of developmental stages were similar to those found in the same general area in the spring. There is insufficient information at this time to consider the effects of environmental conditions on the rate of larval growth and development in *E. gibboides*, but similar variation has been observed in other species of euphausiids (Einarsson 1945; Mauchline 1965).

The range and mean of carapace width in calyptopis stages expressed as percent of carapace length is given in Table 10 as the proportional anterolateral expansion of carapace appears to be a useful character for identification of *E. gibboides*. Comparison by area shows

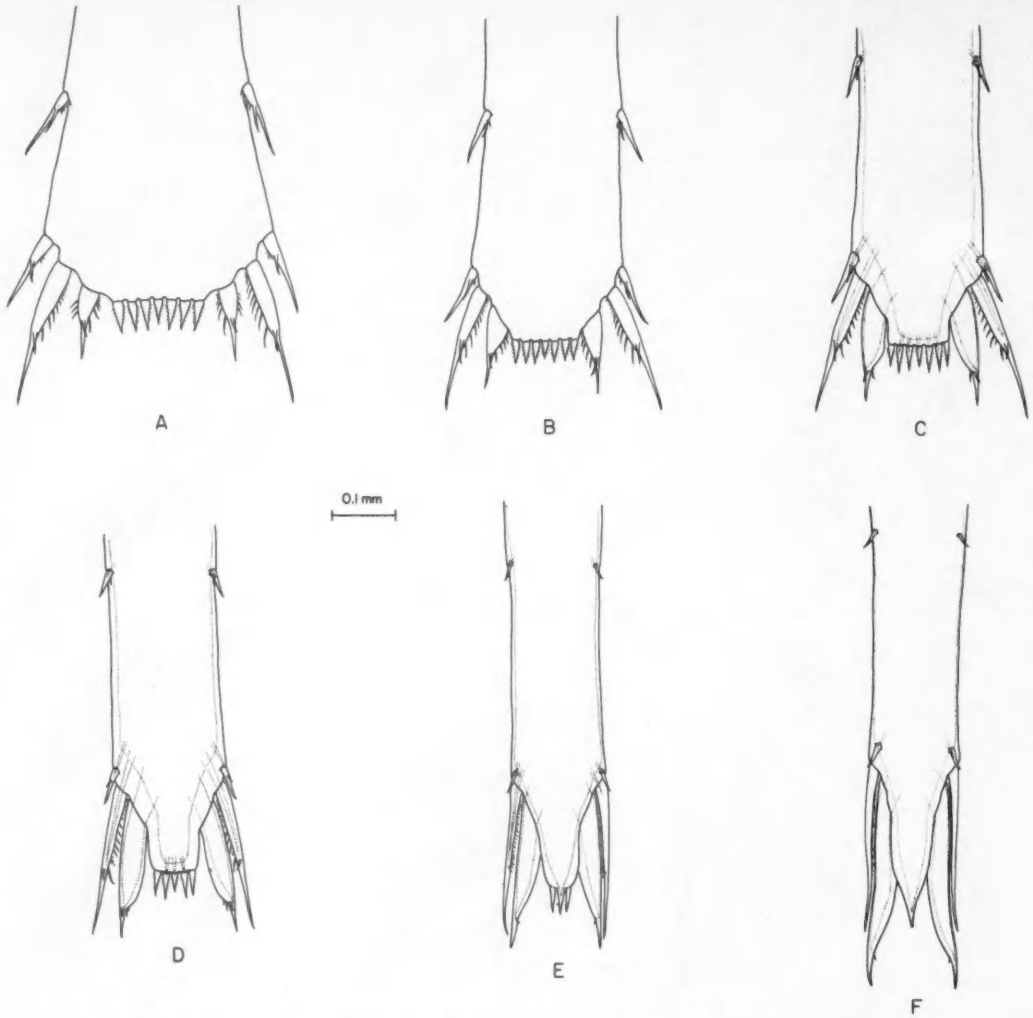

FIGURE 12.—Telson: A, furcilia I; B, furcilia II; C, furcilia III; D, furcilia IV; E, furcilia V; F, furcilia VI.

that the average ratio tends to increase in northern and western Pacific samples.

Juveniles

There was a good series of related juvenile euphausiids in the net haul from station 6304-117.90. Sixty-four were measured and examined in some detail. The smaller juveniles had the distinctive 3-lobed eye described for furcilia stages of *E. gibboides* while some of the larger individuals had the characteristic eye as well as a small dorsal spine on the posterior margin of the 3rd segment of the abdomen and a small dorsal lappet with triangular pointed tip on the margin of the 1st segment of the antennule. The abdominal spine and shape of rudimentary lappet together with the relatively large eye identify the juveniles as *E. gibboides* (Boden et al. 1955). The shape of the eye provides continuity with the

larvae described and confirms their identification.

The juveniles examined ranged from 5.3 to 8.2 mm in total length and a dorsal spine appeared on the 3rd segment of the abdomen at a length of 6.8 mm. A 3-lobed eye was found in a 7.2-mm individual. At 7.0 mm, the constriction between the upper and middle lobes of the eye may disappear; the lower large lobe remains well defined and, although the pigment still appears darker in the lateral position of the middle lobe, the eye becomes increasingly 2-lobed in appearance. The antennule may have a small lappet in 6.3-mm individuals, but the pointed triangular tip was not seen in animals less than 7.0 mm in length, and then it was not always directed outward as in the adult. The lobe and keel of the 2nd and 3rd antennular segments respectively were not developed. A rostral spine may be missing or very small in the early

TABLE 5.—Measurements of nauplius and metanauplius stages.

Stage	Total length (mm)	Width of body (mm)	Width of rostral hood (mm)
Nauplius I:			
Range	0.48-0.53	0.29-0.32	—
$\bar{x}$	0.51	0.30	
SD	0.02	0.01	
n	12	12	
Nauplius II:			
Range	0.51-0.56	0.28-0.32	—
$\bar{x}$	0.53	0.30	
SD	0.01	0.01	
n	12	12	
Metanauplius:			
Range	0.53-0.61	0.28-0.36	0.38-0.45
$\bar{x}$	0.57	0.32	0.42
SD	0.02	0.02	0.02
n	38	38	38

TABLE 6.—Measurements of calyptopis stages.

Stage	Total length (mm)	Carapace width (mm)	Carapace length (mm)
Calyptopis I:			
Range	1.09-1.27	0.59-0.71	0.69-0.79
$\bar{x}$	1.16	0.64	0.72
SD	0.03	0.03	0.02
n	124	124	124
Calyptopis II:			
Range	1.66-1.96	0.65-0.87	0.79-0.93
$\bar{x}$	1.80	0.76	0.86
SD	0.07	0.05	0.03
n	158	158	157
Calyptopis III:			
Range	2.34-2.71	0.75-0.99	0.89-1.09
$\bar{x}$	2.51	0.86	1.00
SD	0.09	0.06	0.05
n	149	149	148

TABLE 7.—Measurements of furcilia stages I-III.

Stage	Total length (mm)	Carapace length (mm)	Rostrum width (mm)	Eye height (mm)
Furcilia I:				
Range	2.85-3.37	0.75-0.85	0.51-0.65	0.24-0.28
$\bar{x}$	3.09	0.80	0.58	0.25
SD	0.10	0.02	0.03	0.01
n	123	104	107	109
Furcilia II:				
Range	3.19-3.94	0.79-0.97	—	0.26-0.32
$\bar{x}$	3.61	0.88		0.29
SD	0.14	0.04		0.01
n	104	98		103
Furcilia III:				
Range	3.80-4.57	0.91-1.09	—	0.30-0.34
$\bar{x}$	4.10	1.02		0.32
SD	0.13	0.04		0.01
n	143	82		83

TABLE 8.—Measurements of furcilia stages IV-VI.

Stage	Total length (mm)	Carapace length (mm)	Eye height (mm)
Furcilia IV:			
dominant — 5 ts (telson spines)			
Range	4.20-4.93	1.01-1.19	0.32-0.38
$\bar{x}$	4.53	1.10	0.34
SD	0.15	0.04	0.02
n	58	56	59
variant — 7 ts			
Range	4.34-4.85	1.05-1.17	0.32-0.36
$\bar{x}$	4.63	1.11	0.34
SD	0.16	0.05	0.01
n	7	5	7
variant — 6 ts			
Range	4.16-4.79	1.03-1.17	0.30-0.36
$\bar{x}$	4.47	1.08	0.34
SD	0.20	0.05	0.02
n	11	10	10
variant — 4 ts			
Range	4.36-4.61	1.07-1.15	0.34-0.36
$\bar{x}$	4.51	1.10	0.34
SD	0.12	0.03	0.01
n	5	4	5
Furcilia V:			
dominant — 3 ts			
Range	4.61-5.41	1.11-1.31	0.36-0.40
$\bar{x}$	4.98	1.20	0.37
SD	0.21	0.06	0.02
n	46	43	46
variant — 5 ts			
Range	4.57-5.25	1.09-1.27	0.36-0.40
$\bar{x}$	4.87	1.17	0.37
SD	0.24	0.05	0.01
n	10	9	9
variant — 4 ts			
Range	4.65-5.33	1.11-1.31	0.34-0.38
$\bar{x}$	4.96	1.19	0.37
SD	0.20	0.06	0.01
n	13	11	13
variant — 2 ts			
Range	5.01-5.29	1.17-1.29	0.36-0.40
$\bar{x}$	5.19	1.25	0.38
SD	0.09	0.04	0.02
n	7	6	8
Furcilia VI:			
dominant — 1 ts			
Range	5.13-5.90	1.17-1.45	0.38-0.44
$\bar{x}$	5.58	1.33	0.40
SD	0.21	0.06	0.02
n	36	35	35
variant — 3 ts			
Range	5.13-5.78	1.19-1.43	0.38-0.40
$\bar{x}$	5.40	1.28	0.40
SD	0.17	0.05	0.01
n	15	14	15
variant — 2 ts			
Range	5.17-5.78	1.23-1.41	0.38-0.42
$\bar{x}$	5.46	1.30	0.40
SD	0.21	0.05	0.01
n	11	10	7

TABLE 9.—Variation in total length of calyptopis stages between the different areas from which samples were studied.

Sample	Calyptopis I				Calyptopis II				Calyptopis III			
	Range	$\bar{x}$	SD	*n*	Range	$\bar{x}$	SD	*n*	Range	$\bar{x}$	SD	*n*
Equatorial Pacific:												
Eastern												
Shellback 187 + 188	1.11-1.17	1.14	0.02	9	1.70-1.94	1.82	0.07	13	2.36-2.63	2.49	0.07	21
North Pacific:												
Eastern												
6304-133.80	1.11-1.21	1.16	0.03	19	1.66-1.82	1.76	0.04	20	2.36-2.55	2.43	0.05	20
6304-120.120	1.09-1.19	1.15	0.02	20	1.66-1.80	1.72	0.04	20	2.34-2.50	2.40	0.05	9
6304-117.90	1.11-1.21	1.15	0.03	20	1.68-1.88	1.77	0.05	20	2.36-2.55	2.45	0.05	20
6304-110.70	1.09-1.19	1.16	0.03	20	1.72-1.86	1.80	0.04	20	2.34-2.67	2.51	0.09	20
6304-70.90 + 100	1.09-1.21	1.15	0.04	21	1.72-1.92	1.82	0.05	20	2.46-2.69	2.56	0.08	11
6304-60.140	1.13-1.27	1.19	0.04	11	1.82-1.98	1.88	0.05	19	2.55-2.71	2.62	0.05	15
6307-117.80	1.09-1.17	1.13	0.02	10	1.72-1.86	1.80	0.05	10	2.40-2.59	2.50	0.06	10
Western												
Transpac 56A + B	—	—	—	—	1.80-1.86	1.84	0.02	6	2.46-2.71	2.58	0.08	11
Transpac 76A	1.11-1.23	1.18	0.06	4	1.68-1.90	1.81	0.06	20	2.44-2.65	2.55	0.06	20

juveniles; it is well developed in larger individuals but never more than one-half the length of the eyestalk in specimens examined.

DISCUSSION

The larvae of many species of the genus *Euphausia* have not been studied but, although preliminary, it may be useful to note ways in which *E. gibboides* larvae differ from related identified forms. The described larvae of *Euphausia* which have features such as armature of carapace or telson similar to those of *E. gibboides* during some phase of development belong to the following species:

Group A *E. brevis* — (Gurney 1942)
E. krohnii — (Sars 1885; Lebour 1926; Frost 1934)
E. diomediae — (Ponomareva 1969)
E. eximia — (author unpubl.)

Group B *E. pacifica* — (Boden 1950; Banse and Komaki 1966[3]; author unpubl.)

Group D *E. longirostris* — (Tattersall 1924; John 1936)
E. spinifera — (Tattersall 1924; John 1936; Sheard 1953)
Euphausia sp. (Ruud 1932; Lebour 1949; Boden 1955)

A metanauplius with marginal fringe of spines on the rostral hood of the carapace is found in *E. brevis, E. krohnii, E. eximia, E. diomediae, E. pacifica,* and Ruud's *E.* sp. as well as in *E. gibboides.* The metanauplius figured by Ruud differs from the others, however, in that the

[3]Banse, K., and Y. Komaki. 1966. Studies of Euphausiidae (Crustacea) off the Washington and Oregon coasts. Annual Report to NSF (Natl. Sci. Found.), Grant No. GB-3360, 6 p. Unpubl.

TABLE 10.—Carapace width expressed as percent of carapace length in calyptopis stages of *E. gibboides* (the number measured is given in Table 9).

Sample	Calyptopis I		Calyptopis II		Calyptopis III	
	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$
Equatorial Pacific:						
Eastern						
Shellback 187 + 188	86.1-91.4	89.3	85.7-92.9	90.1	83.7-91.8	87.7
North Pacific:						
Eastern						
6304-133.80	83.3-91.4	87.4	83.3-90.0	86.0	80.0-85.7	83.1
6304-120.120	83.3-91.2	87.1	82.1-90.0	85.5	80.4-88.6	83.5
6304-117.90	85.3-94.4	88.1	82.5-90.7	86.4	79.6-87.5	83.4
6304-110.70	82.8-91.4	86.8	82.9-90.5	86.5	80.0-87.8	83.8
6304-70.90 + 100	86.1-94.4	90.1	86.0-97.7	91.6	80.0-94.0	86.0
6304-60.140	86.5-91.9	90.1	88.9-95.3	91.0	86.8-92.4	88.8
6307-117.80	87.9-91.4	88.9	87.8-90.5	89.3	90.0-86.3	83.3
Western						
Transpac 56A + B	—	—	90.5-97.6	94.4	88.2-95.8	90.4
Transpac 76A	83.8-91.7	87.8	85.7-93.0	89.6	84.6-90.6	88.0

entire margin of carapace, not only the rostral hood, is spinose. *Euphausia brevis*, *E. krohnii*, and *E. eximia*, unlike *E. gibboides*, have two small dorsal spines on the carapace; *E. diomediae*, the only other species of Group A identified has instead a "sharp eminence" which, as figured (Ponomareva 1969, Figure 1c), is considerably higher and sharper than the dorsal prominence of *E. gibboides*. The metanauplius of *E. pacifica* has a dorsal crest more like that of *E. gibboides* but may prove, with further study, to be consistently smaller; 25 specimens measured from one location by the author ranged from 0.44 to 0.48 mm in total length with an average of 0.46 mm. A metanauplius with fringed rostral hood and two small dorsal spines is figured by Boden (1955) as one of the larval stages of *E. lucens*. It appears, however, that the larvae are those of another species of the genus (Bary 1956), and the form of the metanauplius suggests that it might belong to a species of Group A *Euphausia*.

Calyptopis stages with spinose anterior margin of carapace are found in all of the species listed above except *E. pacifica*. The calyptopes of Group A species may be easily distinguished from those of *E. gibboides* by relative width of carapace; they do not have the anterolateral expansion over the eyes. The carapace of the two species of Group D is wide but, unlike *E. gibboides*, with a very high peaked dorsal crest. Also, the entire margin of the carapace of *E. longirostris* is spinose, the first calyptopis is not described but presumably it does not differ from calyptopes II and III in this respect. The third calyptopis of Lebour's *E.* sp. (1949, Figure 4, 3-4) resembles *E. gibboides* in width of carapace, but the lateral margins of the carapace are spinose. The carapace of the calyptopis I described by Boden (1955, Figure 12) is expanded anterolaterally, but it appears to be proportionally longer than the carapace of *E. gibboides*. The relative lengths of the posterolateral spines of the telson also differ; the 3rd posterolateral spine is relatively short; as figured it is no longer than the terminal spines. The second and third calyptopes of this species have relatively narrow carapaces.

The most useful character for the identification of furcilia stages of *E. gibboides* is the relatively large 3-lobed eye; width of rostral plate and form of pleopods and telson may be helpful as well in differentiating furcilia with spinose anterior margin of carapace. Furcilia of *E. gibboides* may be separated from those of Group A *Euphausia* as follows:

Furcilia with 1 pair of non-setose pleopods — the rostral plate appears to be of greater width in *E. gibboides*;

Furcilia with both setose and non-setose pleopods — in Group A *Euphausia* there is usually only one form and it has 1 setose plus 4 non-setose pairs of pleopods on abdominal segments 1-5 respectively (Sheard (1953) reports numerous variants in the furciliar development of a species identified as *E. recurva*), *E. gibboides* has two forms, 1 setose plus 3 non-setose and 4 setose plus 1 non-setose pair of pleopods;

Furcilia with 5 pairs of setose pleopods — the inner margin of the 3rd (inner) posterolateral spine of the telson is smooth except for tiny distal spinules in larvae of *E. gibboides* and spinose in larvae of Group A.

A single character is sufficient to separate furcilia of *E. gibboides* from those of *E. longirostris* and *E. spinifera*; both Group D species have a dorsal spine on segment 3 of the abdomen beginning in furcilia I. The furcilia with 1 pair of non-setose pleopods figured as *E.* sp. by Lebour (1949, Figure 4, 5-6) differs from *E. gibboides* in relative length of posterolateral spines 2 and 3 of the telson; as drawn they are almost equal in length. The telson of the second furcilia which, like *E. gibboides*, has 1 setose and 3 non-setose pairs of pleopods is not figured, and details of the two forms are not described. The first furcilia figured by Boden (1955, Figure 15) also differs from *E. gibboides* in length of posterolateral spines of the telson; the 2nd pair are almost the same length as the 3rd pair and only a little longer than the 1st pair. The second furcilia of the species has 1 setose and 4 non-setose pairs of pleopods as found in species of Group A *Euphausia*.

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NEW RECORDS OF ELLOBIOPSIDAE (PROTISTA (*INCERTAE SEDIS*)) FROM THE NORTH PACIFIC WITH A DESCRIPTION OF *THALASSOMYCES ALBATROSSI* N.SP., A PARASITE OF THE MYSID *STILOMYSIS MAJOR*

BRUCE L. WING[1]

ABSTRACT

Ten species of ellobiopsids are currently known to occur in the North Pacific Ocean—three on mysids and seven on other crustaceans. *Thalassomyces boschmai* parasitizes mysids of genera *Acanthomysis, Neomysis,* and *Meterythrops* from the coastal waters of Alaska, British Columbia, and Washington. *Thalassomyces albatrossi* n.sp. is described as a parasite of *Stilomysis major* from Korea. *Thalassomyces fasciatus* parasitizes the pelagic mysids *Gnathophausia ingens* and *G. gracilis* from Baja California and southern California. *Thalassomyces marsupii* parasitizes the hyperiid amphipods *Parathemisto pacifica* and *P. libellula* and the lysianassid amphipod *Cyphocaris challengeri* in the northeastern Pacific. *Thalassomyces fagei* parasitizes euphausiids of the genera *Euphausia* and *Thysanoessa* in the northeastern Pacific from the southern Chukchi Sea to southern California, and occurs off the coast of Japan in the western Pacific. *Thalassomyces capillosus* parasitizes the decapod shrimp *Pasiphaea pacifica* in the northeastern Pacific from Alaska to Oregon, while *Thalassomyces californiensis* parasitizes *Pasiphaea emarginata* from central California. An eighth species of *Thalassomyces* parasitizing pasiphaeid shrimp from Baja California remains undescribed. *Ellobiopsis chattoni* parasitizes the calanoid copepods *Metridia longa* and *Pseudocalanus minutus* in the coastal waters of southeastern Alaska. *Ellobiocystis caridarum* is found frequently on the mouth parts of *Pasiphaea pacifica* from southeastern Alaska. An epibiont closely resembling *Ellobiocystis caridarum* has been found on the benthic gammarid amphipod *Rhachotropis helleri* from Auke Bay, Alaska. Where sufficient data are available, notes on variability, seasonal occurrence, and effects on the hosts are presented for each species of ellobiopsid.

The family Ellobiopsidae (Protista (*incertae sedis*)) is a heterogeneous group of parasites and epibionts found on various crustaceans (mostly planktonic) and on the benthic polychaete worm *Nephthys ciliata* Müller. The Ellobiopsidae have been classified at various times as protistans, colorless algae, fungi, or protozoans. The recent work of Galt and Whisler (1970) suggests including the parasitic ellobiopsids among the dinoflagellates.

The parasitic ellobiopsids are multinucleate protistans with reproductive structures outside the host and absorptive portions inside. The reproductive structures often resemble a large mold; consequently, much of the descriptive terminology of ellobiopsids is mycological. The reproductive parts of an ellobiopsid (Figure 1) consist of a short primary stalk passing from the organ of fixation through the cuticle of the host and one or more trophomeres which branch from the primary stalk. The trophomeres in turn bear one or more gonomeres at their distal end.

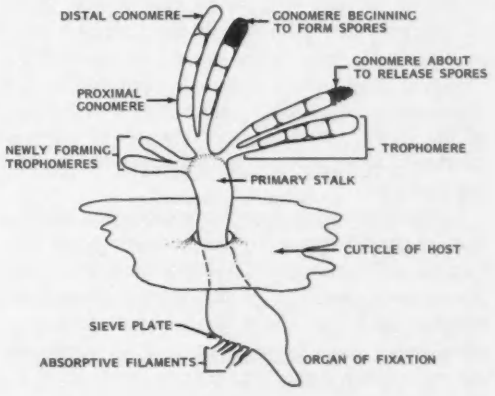

FIGURE 1.—Schematic of an ellobiopsid (*Thalassomyces* sp.)

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The mature distal gonomeres further subdivide to produce motile biflagellate spores (Galt and Whisler 1970).

The internal portion of a parasitic ellobiopsid, the organ of fixation, may be compact (like a bulb or taproot—Figure 1) or may be branching (rhizomorphous). The compact forms bear ridged sieve plates from which extend fine protoplasmic filaments. These filaments are believed to absorb nutrients from the host. The internal portions are difficult to observe without staining and sectioning techniques and have not been used much for taxonomic purposes.

The nonparasitic epibionts of the genus *Ellobiocystis* Coutiere do not have an internal organ of fixation but attach directly to the host's cuticle. These epibionts superficially resemble single trophomeres of the parasitic ellobiopsids but usually have a single gonomere. They are small and attached singly or in clusters to the mouth parts of various shrimps, mysids, and amphipods. Only the morphology of the *Ellobiocystis* spp. has been described. The inclusion of *Ellobiocystis* spp. in the Ellobiopsidae is very questionable.

Other than their morphology, little is known about the ellobiopsids of the genus *Thalassomyces* or their effects on hosts. The development of reproductive spores has been described (Galt and Whisler 1970); however, the mode of infection, time required to mature, and true incidence of infection remain subjects of speculation. Some of the parasitic ellobiopsids sterilize the hosts and probably exert some control on the molting cycle of crustacean hosts. Undoubtedly, the parasites draw heavily on the metabolic resources of the hosts, which conceivably would increase mortality and decrease reproduction in the host populations.

Ellobiopsids were first recognized as a component of the northeastern Pacific fauna when McCauley (1962) recorded *Thalassomyces capillosus* (Fage) as a parasite of the shrimp *Pasiphaea pacifica* Rathbun. Since then eight additional ellobiopsids have been recognized in zooplankton collections from the eastern North Pacific. Only two species of ellobiopsids have been reported from the western North Pacific. In the following discussions for each species, I summarize observations, some new and some from the literature, on the occurrence and hosts of the North Pacific ellobiopsids. I list synonymies only for references to material from the North Pacific. For convenience only, I have treated those ellobiopsids found on mysids first and those found on amphipods, euphausiids, shrimp, and copepods second.

ARTIFICIAL KEY TO ELLOBIOPSIDS FOUND ON MYSIDS

The published keys to the ellobiopsids (Kane 1964; Collard 1966) do not give complete coverage to the ellobiopsids found on mysids. Kane's key is restricted to genera of ellobiopsids, and Collard's key covers only 9 of the 11 known species of *Thalassomyces*. Identification of the known species of *Ellobiocystis*, and *Ellobiopsis* and most *Thalassomyces* is possible by reference to the summaries by Boschma (1949, 1957, 1959). The following key supplements Collard's but treats only the ellobiopsids found on mysids. Two of the species, *T. nouveli* (Hoenigman 1954) and *T. niezabitowskii* (Hoenigman 1960), are known only from the Mediterranean Sea; and *Ellobiocystis caridarum* (Coutiere) while not known from North Pacific mysids is found on Antarctic mysids (Boschma 1949, 1959) and has been found on the North Pacific decapod shrimp *Pasiphaea pacifica*.

1. No root system of attachment to host; attached to oral appendages. Mature parasite consists of single trophomere with one or more gonomeres .... *Ellobiocystis caridarum* (Coutiere)
   Root system of attachment to host; not attached to oral appendages. Mature parasite with many trophomeres branching from stalk(s) . *Thalassomyces* (2)
2. Parasite attached to ventral surface of first abdominal segment. Long pendulous umbellate trophomeres; usually only one gonomere per trophomere (length of mature gonomere 1.5 to over 2 times the diameter) ... *T. fasciatus* (Fage)
   Site of attachment usually dorsal thoracic, but variable. Trophomeres not pendulous; usually more than one gonomere per trophomere (2-4) .....(3)
3. Mature gonomeres flattened spheres. Mean length-diameter ratio less than 1 ..... *T. nouveli* (Hoenigman)
   Mature gonomeres globular to oval. Mean length-diameter ratio greater than 1 ....(4)

4. Primary stalks widely spaced when more than one per host. Mature gonomere length-diameter ratio 0.7-1.9 (mean about 1.2) .....(5)
   Primary stalks closely spaced when more than one per host. Mature gonomere length-diameter ratio 1.5-2.4 (mean about 2) .....*T. albatrossi* n.sp.
5. Mature terminal gonomere shape ellipsoid, with the distal end the same size as the proximal end, to spherical ....*T. boschmai* (Nouvel)
   Mature terminal gonomere shape ovoid, with the distal end smaller than the proximal end, to spherical ....*T. niezabitowskii* (Hoenigman)

ELLOBIOPSIDS OF NORTH PACIFIC MYSIDS

Thalassomyces boschmai (Nouvel 1954)

Thalassomyces sp.—Wing (1965), Hoffman and Yancey (1966), Thorne (1968).
Thalassomyces boschmai—Galt and Whisler (1970), Vader (1973b).

Ellobiopsids of the genus *Thalassomyces* have been observed on Mysidae from Alaska (Wing 1965; Hoffman and Yancey 1966); from Puget Sound (Thorne 1968); and from southern British Columbia (J. Galt, Friday Harbor Laboratory, University of Washington, Friday Harbor, WA 98250, pers. commun.). New collections of Alaska mysids (Table 1) plus supplementary material from Puget Sound enabled me to identify these ellobiopsids as *T. boschmai*.

Characteristics of *T. boschmai*

The identification of *Thalassomyces* spp. parasitizing mysids is based on external portions so variable that for definitive identifications, several characters must be examined. The external characters used to identify a species are the total size or height of the parasite, length of trophomeres, number of trophomeres per primary stalk, number of gonomeres per trophomere, and size and shape of gonomeres. The number of primary stalks and the site of attachment are also useful characteristics. Differences between specimens from different localities may be associated with local races and may to some extent be phenotypically associated with the host species.

TABLE 1.—Records of *Thalassomyces boschmai* found on mysids in Alaska, 1963-67.

Area, collection number, and species of host	Number of mysids with *T. boschmai*	Number of *T. boschmai*
Little Port Walter[1]		
AB66-243		
Acanthomysis pseudomacropsis	4	4
Neomysis kadiakensis	70+	80+
AB66-244		
Acanthomysis pseudomacropsis	2	2
Neomysis kadiakensis	9+	23+
Auke Bay[2]		
AB65-108		
Acanthomysis pseudomacropsis	8	8
Neomysis kadiakensis	8	10+
Katlian Bay[3]		
AB67-45		
Acanthomysis pseudomacropsis	1	1
AB67-46		
Meterythrops robusta	2	2
Kachemak Bay[4]		
Acanthomysis pseudomacropsis	3	6

[1]Taken in light-baited trap; lat. 56°23'N, long. 134°39'W; 7-8 September 1966.
[2]Taken in light-baited trap; lat. 58°21'N, long. 134°40'W; 24 June 1964.
[3]Taken in Isaacs-Kidd mid-water trawl; lat. 57°10'N, long. 135°21'W; 21 April 1967.
[4]Collection of Hoffman and Yancey (1966); lat. 59°27'N, long. 151° 33'W; October, December 1963 and February 1964. No collection number because material was lost.

The height of the North Pacific *T. boschmai* ranges from 0.75 to 1.70 mm; most of the specimens are between 1.30 and 1.50 mm. The maximum height is larger than the 1.25 mm given by Hoenigman (1954) for *T. boschmai* found on *Leptomysis gracilis* G. O. Sars, but in the Pacific, host mysids are much longer than the Mediterranean *Leptomysis* (13 mm). *Neomysis kadiakensis* Ortman are often over 20 mm long. Boschma (1959) noted a positive relationship between the size of the host and the size of the parasite *T. fagei* (Boschma) on euphausiids.

Mature trophomeres constitute most of the external mass of an ellobiopsid parasite. Within a parasite, the lengths of the trophomeres appear uniform, but they vary greatly between parasites. Lengths of trophomeres from 18 parasites found on *Acanthomysis pseudomacropsis* (Tattersall) and *N. kadiakensis* were from 0.72 to 1.32 mm. Because gonomeres are lost during sporulation, old trophomeres are generally 0.3 to 0.7 mm shorter than those that still have three or four gonomeres.

The number of trophomeres per primary stalk depends on the state of development and the condition of preservation. Dichotomous branching close to the point where the trophomeres

join the primary stalk makes it difficult to determine the number of trophomeres in a dense tuft, or the number that may be developing, or those that may have been lost. Counts of trophomeres on 21 *T. boschmai* from southeastern Alaska ranged from 13 to 46 (mean 28.6). Hoffman and Yancey (1966) examined six parasites which had 7 to 20 trophomeres each. Nouvel and Hoenigman (1955) found a maximum of 32 (mode 16) trophomeres for 21 Mediterranean *T. boschmai* from Cabo do Palos, Spain.

The number of gonomeres on a mature trophomere of *T. boschmai* is usually three, rarely four. Trophomeres having no gonomeres or up to two are immature, damaged, or are degenerating after sporulation. Degenerating trophomeres may be recognized by the small rudiments of protoplasm left after sporulation (Nouvel and Hoenigman 1955).

The size and shape of the gonomeres, especially the distal gonomere (Figure 1), are used as taxonomic characters, but most descriptions give little information on the variability of gonomere characters. I measured gonomere lengths and diameters and computed length-diameter ratios for 10 *T. boschmai* from each of two sites in southeastern Alaska and one in Puget Sound for comparison with data from central Alaska (Hoffman and Yancey 1966) and the western Mediterranean (Nouvel and Hoenigman 1955) (Table 2). The ranges of lengths and diameters were greater in specimens from southeastern Alaska and Puget Sound than in those from central Alaska or the Mediterranean, although the mean sizes were similar. A weighted *t*-test (Ostle 1963) confirmed (95% level) that ellobiopsids from different host species of mysids but within the same collection belong to the same statistical population; that is, all the ellobiopsids within each collection may be considered as one species. Tests for significant differences between means indicated that *T. boschmai* from the three collections were from different populations, but the broad overlap of gonomere size ranges, especially the length-diameter ratios (Figure 2), makes specific distinction unwarranted.

Occasionally an ellobiopsid will form more than one primary stalk by internal budding. This produces two or more stalks which separately penetrate the host's cuticle. The stalks are usually less than 1 mm apart. Budding described for *T. boschmai* and *T. nouveli* in the Mediterranean (Hoenigman 1954) is rare in the North Pacific *T. boschmai*. I examined 130 ellobiopsids from the North Pacific and found only one instance of apparent budding—a *T. boschmai* on an *A. pseudomacropsis* from Katlian Bay, Alaska.

On mysids, *T. boschmai* usually occur either on the dorsal surface of the host's carapace or on the last thoracic segment, although some are found on the dorsal, lateral, or ventral surface of the abdomen. In contrast, the most frequent sites of attachment on *L. gracilis* are the frontal plaque and rostral areas (Hoenigman 1954; Nouvel 1954; Nouvel and Hoenigman 1955).

Less than 10% of the parasitized mysids I examined had more than one *T. boschmai*. In one case a mysid had four ellobiopsids, and another mysid bore scars from four ellobiopsids. Hoenigman (1954) observed one *L. gracilis* with seven *T. boschmai*. When two or more ellobiopsids occur on a mysid, they usually are widely separated; one ellobiopsid may be on the thorax and the other(s) may be on various parts of the abdomen or rostrum. Two of the three hosts described by Hoffman and Yancey (1966) had both ellobiopsids on the carapace; in the third, the second ellobiopsid was on the abdomen.

Observations of Living *T. boschmai*

Collard (1966), Vader and Kane (1968), and Galt and Whisler (1970) have described living *Thalassomyces* spp. I briefly observed three living *T. boschmai* on *A. pseudomacropsis* from the first Auke Bay collection (AB65-108). In the live *T. boschmai*, the external portions were transparent and colorless except for a slight yellow tint at the base of the primary stalk. Perhaps the tinting is caused by the same melanic pigment deposited by the host at the margin of the pore through the host's cuticle. Deposition of pigments at the site of injury or parasitism is a frequent occurrence among crustaceans. The parasites stand out from the host's carapace, which gives the appearance of a flexible cluster of grapes that twist and turn slightly as the host swims. The live ellobiopsids I observed had about 40 trophomeres each with one to four gonomeres per trophomere. Many distal gonomeres were pebbled as described by Collard (1966) and Galt and Whisler (1970). I observed that some gonomeres had the amorphous drop of protoplasm described by Collard, but I did not find the

TABLE 2.—Ranges, means, and 0.95 confidence intervals (CI) of means for lengths, diameters, and length-diameter ratios of terminal gonomeres of *Thalassomyces boschmai* parasitizing mysids in collections from the western Mediterranean, Washington, southeastern Alaska, and central Alaska.

Host mysid and number of gonomeres measured	Length (mm)			Diameter (mm)			Ratio length to diameter		
	Range	Mean	0.95CI	Range	Mean	0.95CI	Range	Mean	0.95CI
Western Mediterranean (Cabo do Palos, Spain)									
Leptomysis gracilis[1]									
8	0.240-0.300	0.258		0.205-0.240	0.228		1.00-1.46	1.14	
7	0.155-0.185	0.172		0.150-0.170	0.158		1.00-1.17	1.09	
Total —	0.155-0.300	—	—	0.135-0.250	—	—	—	—	—
Washington (Puget Sound)									
Neomysis kadiakensis									
1	—	0.208		—	0.250		—	0.83	
5	0.24-0.27	0.251		0.19-0.24	0.223		0.96-1.44	1.14	
7	0.21-0.26	0.232		0.16-0.22	0.180		1.04-1.44	1.31	
4	0.30-0.36	0.319		0.26-0.28	0.269		1.12-1.35	1.19	
5	0.32-0.36	0.339		0.27-0.30	0.282		1.09-1.33	1.21	
4	0.24-0.28	0.251		0.18-0.24	0.200		1.20-1.33	1.26	
3	0.23-0.26	0.239		0.22-0.24	0.231		0.96-1.10	1.03	
4	0.30-0.33	0.305		0.24-0.29	0.260		0.98-1.22	1.14	
3	0.25-0.28	0.262		0.18-0.20	0.193		1.32-1.40	1.36	
1	—	0.305		—	0.190		—	1.61	
Total 37	0.21-0.36	0.273	±0.014	0.18-0.30	0.228	±0.014	0.96-1.61	1.22	±0.06
Southeastern Alaska (Little Port Walter)									
Acanthomysis pseudomacropsis									
10	0.19-0.22	0.198		0.17-0.22	0.198		0.94-1.00	1.00	
Neomysis kadiakensis									
10	0.24-0.29	0.263		0.20-0.26	0.223		1.00-1.41	1.18	
10	0.22-0.25	0.235		0.19-0.24	0.224		0.90-1.25	1.05	
10	0.22-0.29	0.259		0.22-0.26	0.236		0.90-1.25	1.10	
10	0.29-0.34	0.314		0.26-0.31	0.295		1.00-1.17	1.06	
10	0.24-0.38	0.298		0.24-0.34	0.287		0.71-1.17	1.04	
10	0.22-0.26	0.242		0.19-0.23	0.210		1.00-1.25	1.15	
10	0.31-0.41	0.350		0.24-0.29	0.275		1.08-1.42	1.28	
10	0.26-0.36	0.278		0.24-0.31	0.241		1.00-1.44	1.15	
10	0.19-0.24	0.214		0.19-0.24	0.206		0.90-1.12	1.03	
10	0.19-0.26	0.226		0.19-0.24	0.204		1.00-1.25	1.11	
10	0.22-0.29	0.247		0.17-0.22	0.197		1.00-1.67	1.26	
Total 120	0.19-0.41	0.260	±0.012	0.17-0.34	0.233	±0.009	0.71-1.67	1.10	±0.04
Southeastern Alaska (Auke Bay)									
Acanthomysis pseudomacropsis									
11	0.15-0.31	0.205		0.13-0.23	0.168		0.79-1.71	1.23	
11	0.17-0.28	0.228		0.14-0.18	0.156		1.21-1.87	1.46	
13	0.24-0.32	0.291		0.18-0.26	0.230		1.08-1.39	1.27	
10	0.13-0.17	0.157		0.14-0.16	0.150		0.86-1.14	1.04	
10	0.24-0.38	0.319		0.22-0.31	0.261		0.84-1.73	1.24	
10	0.27-0.29	0.282		0.18-0.24	0.212		1.21-1.56	1.34	
5	0.27-0.30	0.280		0.17-0.29	0.202		0.96-1.70	1.44	
Neomysis kadiakensis									
10	0.20-0.25	0.231		0.15-0.23	0.173		1.08-1.39	1.25	
Total 80	0.13-0.38	0.230	±0.019	0.13-0.31	0.181	±0.014	0.79-1.87	1.28	±0.05
Central Alaska (Kasitsna Bay)									
Acanthomysis pseudomacropsis[2]									
—	—	—	—	0.14-0.21	0.17	—	—	—	—

[1]Data from Nouvel and Hoenigman (1955). The authors gave the total length and diameter ranges shown but did not give the total number of gonomeres used to figure these ranges.
[2]Data from Hoffman and Yancey (1966).

gonomeres of *T. boschmai* to be adherent as Collard found for *T. californiensis* Collard.

Effect of Host

Adult and juvenile mysids are parasitized by *T. boschmai*. I made no histological studies of sterilization, but in the 130 parasitized mysids examined, no brooding females occurred and reduced oostegites were common. Sterilization may not always result, for Nouvel and Hoenigman (1955) found a brooding female *L. gracilis* parasitized by *T. boschmai*. Because the length of time for development of the parasite or the eggs of the mysids is not known, the specimen observed by Nouvel and Hoenigman may have deposited her eggs before being parasitized. The parasite must also affect the host's molting and growth because

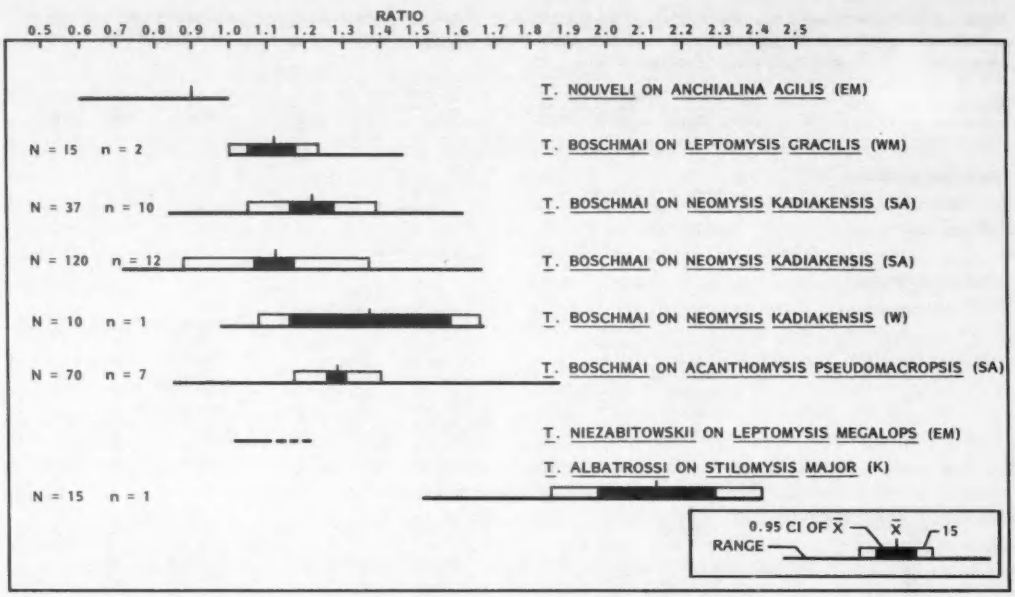
RATIO
0.5 0.6 0.7 0.8 0.9 1.0 1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8 1.9 2.0 2.1 2.2 2.3 2.4 2.5
T. NOUVELI ON ANCHIALINA AGILIS (EM)
N = 15 n = 2
T. BOSCHMAI ON LEPTOMYSIS GRACILIS (WM)
N = 37 n = 10
T. BOSCHMAI ON NEOMYSIS KADIAKENSIS (SA)
N = 120 n = 12
T. BOSCHMAI ON NEOMYSIS KADIAKENSIS (SA)
N = 10 n = 1
T. BOSCHMAI ON NEOMYSIS KADIAKENSIS (W)
N = 70 n = 7
T. BOSCHMAI ON ACANTHOMYSIS PSEUDOMACROPSIS (SA)
T. NIEZABITOWSKII ON LEPTOMYSIS MEGALOPS (EM)
T. ALBATROSSI ON STILOMYSIS MAJOR (K)
N = 15 n = 1
0.95 CI OF $\bar{X}$
$\bar{X}$
15
RANGE

FIGURE 2.—Length-diameter ratios of *Thalassomyces* found on Mysidae from the eastern Mediterranean (EM), western Mediterranean (WM), Washington (W), southeastern Alaska (SA), and Korea (K). The horizontal line represents the sample range, the vertical line the sample mean; the black rectangle represents the 0.95 confidence limits of the mean, and the distance from the mean line to the edge of the white rectangle represents 1 standard deviation; N = number of gonomeres measured and n = number of parasites (the numbers are unknown for *T. nouveli* and *T. niezabitowskii*).

the external portions of the parasite could hardly be retained during a molt. The control over molting could be by starvation as postulated by Wickstead (1963) or by disturbance of the host's neuroendocrine system as postulated by Hoffman and Yancey (1966). The close association of other *Thalassomyces* with the nervous system (Boschma 1959; Kane 1964; Collard 1966) or the gonadal areas (Einarsson 1945; Boschma 1959) suggests some hormonal control over growth, molting, and maturation of the host.

The behavior of the parasitized mysids is not noticeably affected. The swimming speed and maneuverability of parasitized and nonparasitized mysids appear to be the same; flexing and twisting of the ellobiopsids as they are dragged through the water apparently do not affect the host.

Hosts of *T. boschmai*

This species has been recorded as a parasite of *L. gracilis* and *Gastrosaccus lobatus* (Nouvel) in the Mediterranean Sea (Nouvel 1954; Hoenigman 1954, 1960, 1963; Nouvel and Hoenigman 1955). Five mysids are known as hosts of *T. boschmai* in the eastern North Pacific. In Puget Sound, *Acanthomysis macropsis* (Tattersall), *A. nephrophthalma* Banner, and *N. kadiakensis* are hosts (Thorne 1968). In Alaska, *A. pseudomacropsis* (Wing 1965, Hoffman and Yancey 1966), *N. kadiakensis* (Wing 1965), and *Meterythrops robusta* S. I. Smith have been observed parasitized by *T. boschmai*. *Meterythrops robusta* is a new host record.

Seasonal Occurrence

Thorne (1968) reported a seasonal pattern of incidence of infection by mysids (the percentage of *N. kadiakensis* with ellobiopsids) by *T. boschmai* at Port Orchard, Puget Sound, Wash. The incidence of infection at Port Orchard was low in the winter and spring (1 to 8% of adults, 1 to 21.5% of immatures) and rose in the late summer to a maximum in October (17% of adults, 35% of immatures). A seasonal pattern of infestation is not clear in the Alaska material. Although the

number of infected hosts and the proportion of hosts with more than one parasite were greatest in the late summer, this may be an artifact of sampling methods. Long-term sampling with plankton nets at Auke Bay and Little Port Walter has not captured parasitized mysids and generally has not taken large numbers of mysids. The light-baited trap is exceptionally effective in capturing mysids but has been used only in summer. Although no quantitative data are available for the Auke Bay sample (AB65-108—Table 1), it contained several thousand mysids. The two Little Port Walter collections contained about 9,000 and 7,000 mysids respectively (Table 3).

Thalassomyces albatrossi n.sp.

?*Amallocystis fasciatus*—Tattersall (1951), Boschma (1959).
Thalassomyces fasciatus—Collard (1966).
Thalassomyces n.sp.—Vader (1973b).

Type location:[2] *Albatross* stn. 4867, lat. 36° 31′N, long. 129°46′E; depth 150 fathoms; 1 August 1906. USNM 82439.

Holotype: One slide with several gonomeres and trophomeres separated and mounted whole. Remainder left on the host. Host: *Stilomysis major* Tattersall, female, 26 mm long; carapace length, 7.9 mm.

Paratype: Immature, bearing two tufts or stalks of trophomeres, intact on host. Host: *S. major*, female, from USNM 81268.

Location: *Albatross* stn. 4862, lat. 36°20′N, long. 129°50′E; depth 184 fathoms; 31 July 1906.

Disposition of types: Holotype and paratype deposited in Division of Crustacea, Smithsonian Institution, U.S. National Museum, Washington, D.C., as Type USNM 24366 and USNM 24367.

[2]The locale on the original collection labels is Cape Clonard, Japan. Political changes since 1906 have resulted in name changes, the area now being referable to near Yonghae, South Korea.

Specific Diagnosis

The external portion of the parasite is visible as one to four tufts of trophomeres located middorsally on the host's thorax. In the mature parasite, each tuft contains up to 50 trophomeres, which arise by close dichotomous branching from the primary stalk. Trophomeres are 0.80 to 1.70 mm long. Each trophomere bears one to four gonomeres, usually three. Mature distal gonomeres are oval to elongate in shape—0.4 to 0.7 mm long and 0.25 to 0.35 mm in diameter. The length of the distal gonomere is 1.5 to 2.4 times the diameter. The penultimate and proximal gonomeres are usually shorter than the distal gonomere but have about the same diameter.

[Diagnosis Propria: Pars parasiti externa apparet unus ad quattuor racemi trophomerorum medio dorso in animalis thorace positi. In maturo parasito, unusquisque racemorum fert ad quinquaginta trophomera, quae in duas partes proximas ex stirpe principali dividuntur. Trophomera sunt 0.80 ad 1.70 mm longa. Unumquidque trophomerorum fert unum ad quattuor gonomera, plerumque tria. Matura gonomera distalia sunt conformatione ovata ad praelonga—0.4 ad 0.7 mm longa et 0.25 ad 0.35 mm per medium. Longitudo gonomeri distalis est 1.5 ad 2.4 eius gonomeri dimetientes. Gonomera paenultima et proximalia sunt plerumque breviora quam gonomera distali, sed sunt per medium fere eadem.]

This species differs most clearly from other closely related *Thalassomyces* (*T. boschmai*, *T. niezabitowskii*, and *T. nouveli*) found on mysids by having much longer terminal gonomeres (which exceed 0.4 mm), a more elongate shape of the gonomeres, and three or four tufts of

TABLE 3.—Species and number of mysids and incidence of *Thalassomyces boschmai* in two light-baited trap samples at Little Port Walter, 7-8 September 1966.

Species	AB66-243 (2-h set)		AB66-244 (7-h set)	
	Number of mysids caught	Number of mysids parasitized by *T. boschmai*	Number of mysids caught	Number of mysids parasitized by *T. boschmai*
Acanthomysis pseudomacropsis	1,680	4	4,960	2
Acanthomysis sp.	1,600	0	290	0
Neomysis kadiakensis	5,630	70+	1,160	9+
Mysis litoralis	<20	0	740	0
Total	8,930	74+	7,150	11+

trophomeres rather than one or two per parasite. It differs from *T. fasciatus* by being attached to the dorsum of the host's thorax rather than the ventral abdomen, by bearing multiple gonomeres on each trophomere rather than one or rarely two, and by having much shorter lengths of the trophomeres (not including the gonomeres —about half that of *T. fasciatus*).

Description of Holotype

Externally, the holotype consists of three tufts of trophomeres attached to the dorsal carapace (Figure 3). The prior existence of a fourth tuft is indicated by a scar on the host's carapace. Dense packing of the trophomeres and the apparent loss of some by breakage during preservation and handling made it impossible to determine the exact number of trophomeres in each tuft. Examination at 40× magnification indicated the following approximate numbers: 45 in the left anterior tuft, 20 in the left posterior tuft, and 35 in the right posterior tuft. The trophomeres branch dichotomously close to the primary stalk, which gives an appearance of many trophomeres arising directly from the primary stalk. The trophomeres are of various lengths—0.8 to 1.7 mm. Each trophomere (Figure 4a, b) is composed of a short basal portion and one to three gonomeres, usually three. A few trophomeres appear to have lost a fourth gonomere.

The gonomeres (Figure 4) vary in shape from oval to elongate; a few distal gonomeres are small and cone shaped. The penultimate and proximal gonomeres vary considerably in length but are of similar diameter to the normal distal gonomeres (0.25 to 0.32 mm). The dimensions of 15 distal gonomeres (measured in situ) are summarized in Table 4.

The host specimen, which was preserved in ethyl alcohol, was partially dehydrated, brittle, and broken at the third and fourth thoracic

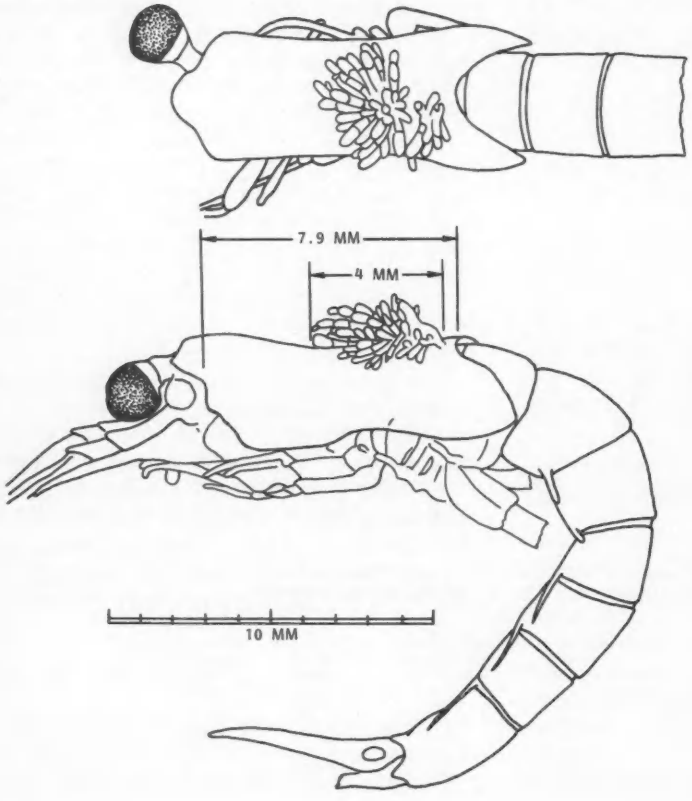

FIGURE 3.—Holotype of *Thalassomyces albatrossi* n.sp. on *Stilomysis major*. A. Lateral view. B. Dorsal view.

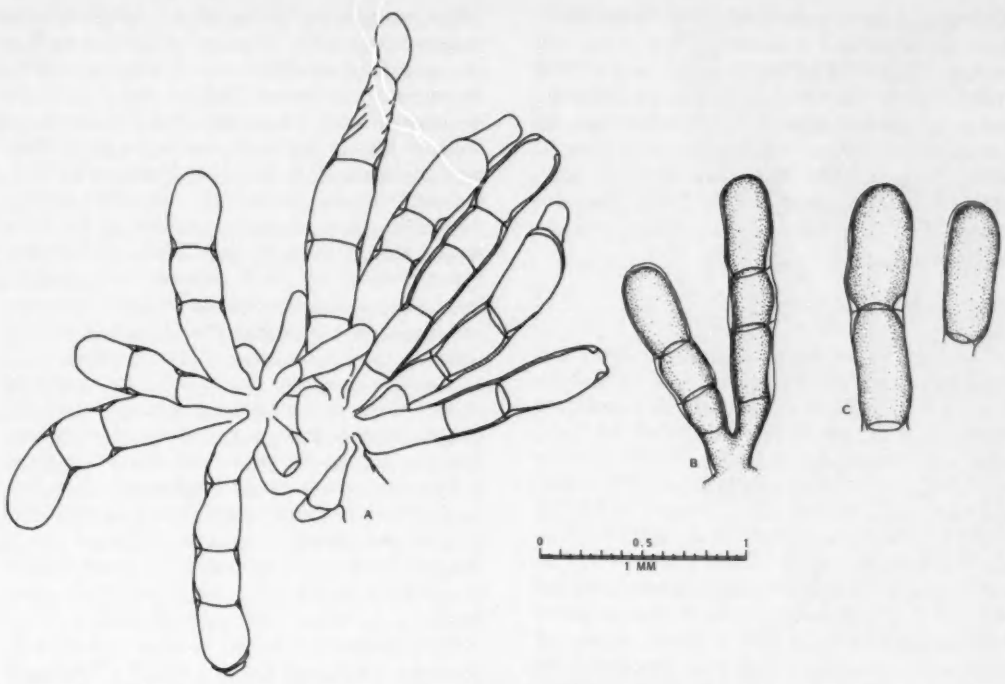

FIGURE 4.—Holotype of *Thalassomyces albatrossi* n.sp. A. Cluster of trophomeres. B. Pair of trophomeres, each bearing three gonomeres. C. Separate gonomeres.

TABLE 4.—Dimensions of 15 distal gonomeres from holotype of *Thalassomyces albatrossi* n.sp.

Dimension	Range (mm)	Mean (mm)	SD	0.95 CI of mean
Length	0.41-0.68	0.57	0.07	0.04
Diameter	0.25-0.32	0.27	0.03	0.01
Length-diameter ratio	1.5-2.4	2.1	0.3	0.15

segments—the site of attachment to the ellobiopsid. Histological studies were not done because of this damage. Each of the three primary stalks passes through the carapace of the host. Just inside the carapace there is a connection between the left pair of stalks. A similar connection between the right stalk and the left anterior stalk is indicated by a torn piece of an ellobiopsid projecting from the right stalk toward the left anterior stalk. Below the connection between the left pair of stalks is a small (about 1.5 mm long) elongate conical organ of absorption (fixation), which appears to have passed through or between the ovaries of the host. The organ is similar to that figured for *T. nouveli* by Hoenigman (1954).

Description of Paratype

The paratype is an immature ellobiopsid consisting of two primary stalks which pass through the carapace of the host. None of the trophomeres bear more than two gonomeres; several of them have no gonomeres and appear to have been damaged in handling or by drying after preservation. Because of the withered state of the specimen, no accurate measurements of either the trophomeres or the gonomeres can be made. The gonomeres on one of the stalks are, however, thinner than those on the other. No sporulating gonomeres are present.

Specimens Examined

In the discussion that followed his description of *S. major*, Tattersall (1951) states that two specimens were parasitized by an ellobiopsid resembling *T. fasciatus* (Fage). Subsequent authors accepted this tentative identification by Tattersall, but my examination of the ellobiopsids from his material revealed only *T.*

albatrossi. I have examined 15 *S. major* from three of Tattersall's collections. Two of the collections (USNM 82439—2 *S. major*, and USNM 81268—10 *S. major*) contained the holotype and paratype respectively of *T. albatrossi*. In the third collection (USNM 82440—three *S. major; Albatross* stn. 4861; lat. 36°19'N, long. 129°47'E; 163 fathoms; 31 July 1906) I found a female *S. major* bearing four scars from an ellobiopsid.

Effect on the Host

The mysid specimens bearing the type and paratype ellobiopsids were females of mature size but with reduced oostegites. This apparent sterilization agrees with observations of Fage (1941), Einarsson (1945), and Nouvel (1941), who noted that ellobiopsids sterilize their hosts. A scarred mature female *S. major* in USNM 82440 was brooding young but appeared to have been parasitized earlier by an ellobiopsid. The scars consisted of holes in the carapace, probably caused by the primary stalks of the parasite. Each of the four holes had a heavy deposit of pigment at the margin that was surrounded by a clear area. Thus, it appears that the sterilization by ellobiopsids may be temporary, as suggested by Wickstead (1963), or it may be influenced by the age of the host at the time of infection.

Distribution

The new species has been reported only from the eastern coast of Korea, the type locality of the parasite and its host.

Derivation of Name

The specific name *albatrossi* is selected to honor the U.S. steamer *Albatross*, the vessel from which the parasitized mysids were collected. The many biological collections made from the *Albatross* during 39 yr of service to the U.S. Fisheries Commission and later to the U.S. Bureau of Fisheries have been of immeasurable value in the investigation of life in the oceans.

Thalassomyces fasciatus (Fage 1936)

Amallocystis fasciatus—Pequegnat (1965).
Thalassomyces fasciatus—Vader (1973b).

Thalassomyces fasciatus is a large species known to parasitize only lophogastrid mysids of the genus *Gnathophausia*. Pequegnat (1965) found it on *G. ingens* (Dohrn) and *G. gracilis* Willemoes-Suhm off central Baja California. It has also been collected in the Santa Cruz Basin off California (S.B. Collard, Marine Environmental Sciences Consortium, Dauphin Island, AL 36528, pers. commun.). Boschma (1959) recorded this ellobiopsid on *G. gigas* Willemoes-Suhm from Spain; on *G. ingens* from Morocco, the Lesser Antilles, and the Maldive Islands; and on *G. zoea* Willemoes-Suhm from Portugal, Guiana, the Fiji Islands, and New Zealand.

Thalassomyces fasciatus attaches to the ventral surface of the first abdominal somite of the host. The gonomeres are oval and about twice as long as wide (0.4 by 0.2 mm), and normally, there is only one gonomere per trophomere (Boschma 1959). The trophomeres are long (1.5 mm total length) and joined in groups of five or six to the primary stalk (Fage 1941). In these aspects *T. fasciatus* differs from the *T. albatrossi* n.sp. found on *S. major* by Tattersall (1951), which were erroneously believed to be *T. fasciatus* by Boschma (1959) and Collard (1966). The size of the gonomeres and total length of trophomeres (including the gonomeres) in the two species are similar, although my specimens of *T. albatrossi* have a greater number of gonomeres per trophomere than *T. fasciatus* and therefore do not appear to be as long and pendulate.

ADDITIONAL RECORDS OF NORTH PACIFIC ELLOBIOPSIDS

Besides the three species of *Thalassomyces* found on mysids, seven other ellobiopsids have been found on crustaceans in the North Pacific. The following sections summarize current knowledge about the hosts and distribution of these seven ellobiopsids.

Thalassomyces marsupii Kane 1964

Thalassomyces marsupii—Galt and Whisler (1970), Vader (1973b).

Thalassomyces marsupii is found inside the marsupium of host amphipods. The mature parasites resemble compact egg masses. Usually the whitish spherical gonomeres are smaller than the

eggs of the host species. An infected amphipod carries one, rarely two, parasites. The mature parasites may completely fill the marsupium of small amphipods and occasionally protrude beyond the marsupium of an immature host. In large or heavily pigmented amphipods, *T. marsupii* is easily overlooked unless specifically searched for. On male amphipods, *T. marsupii* are more easily noticed although they are often obscured by the thoracic legs and coxal plates of the host.

Thalassomyces marsupii parasitizes both pelagic and benthic amphipods and appears to have a worldwide distribution. The recorded pelagic hosts are hyperiids of the genus *Parathemisto: P. gaudichaudii* (Guerin) in the North Atlantic, Benguela Current, and Southern Ocean (Kane 1964); *P. abyssorum* Boeck in the North Atlantic (Vader and Kane 1968) and Arctic (Tencati and Geiger 1968); *P. gracilipes* Norman in the North Sea (R. A. McHardy, Department of Oceanography, The University, Southampton, England, pers. commun.); and *P. pacifica* Stebbing in Puget Sound (Galt and Whisler 1970). A similar parasite has been observed on *Cystisoma* sp., a hyperiid, in the North Pacific (T. H. Bowman, Division of Crustacea, Smithsonian Institution, U.S. National Museum, Washington, DC 20560, pers. commun.). The recorded epibenthic gammarid hosts of *T. marsupii* are: *Eusirus leptocarpus* G. O. Sars, *E. longipes* Boeck, *Rhachotropis aculeata* (Lepechin), *R. macropus* G. O. Sars, and *R. helleri* Boeck, all family Eusiridae, from several North Atlantic locales (Vader and Kane 1968).

I have observed *T. marsupii* on three species of amphipods in southeastern Alaska: the hyperiids *Parathemisto pacifica* and *P. libellula* (Lichtenstein) and the pelagic gammarid *Cyphocaris challengeri* Stebbing (family Lysianissidae). *Parathemisto libellula* and *C. challengeri* are new host records as well as geographic range extensions for *T. marsupii*. The parasitized amphipods were collected with a 1.8-m Isaacs-Kidd mid-water trawl by the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) in Lynn Canal and Chatham Strait. The sampling program continued from March 1964 to February 1967; each year eight stations (Figure 5) were sampled quarterly at depths of 15 and 100 m. Beginning with the August 1965 samples, I kept records of the occurrence of *T. marsupii* on

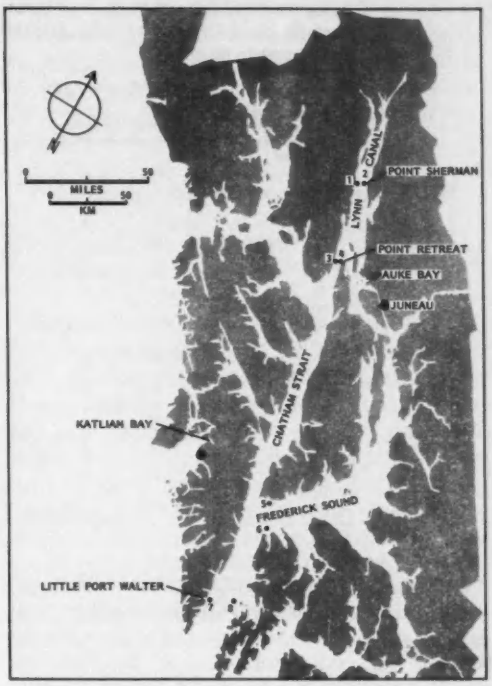

FIGURE 5.—Locations in southeastern Alaska where ellobiopsids were collected.

Alaska amphipods. The parasitized amphipods were found mostly in the 15-m samples. *Cyphocaris challengeri* was the most frequent host, and the highest incidence of parasitism occurred in the August samples (Table 5).

The internal portions of the parasite were not examined, but the external morphology, size, and site of attachment correspond closely to Kane's original description. Most of the specimens I examined were forming gonomeres. A few gonomeres had begun cleavage to form spores. The sporulating gonomeres were not as deeply sculptured nor as dark as those described by Kane (1964).

Thalassomyces fagei (Boschma 1948)

Thalassomyces fagei—Hoffman and Yancey (1966), Komaki (1970), Vader (1973b).

The euphausiid *Thysanoessa raschii* (M. Sars) is the most common host of *Thalassomyces fagei* in Alaska waters. I have examined parasitized

TABLE 5.—Occurrence of *Thalassomyces marsupii* on three species of amphipods taken in quarterly sampling with a 1.8-m Isaacs-Kidd mid-water trawl (August 1965 to February 1967) in southeastern Alaska.

Cruise date and station number	*Cyphocaris challengeri*		*Parathemisto libellula*		*Parathemisto pacifica*	
	Number collected	Number parasitized	Number collected	Number parasitized	Number collected	Number parasitized
August 1965						
1	107	3	80	0	4	0
2	176	5	89	0	3	0
3	10	1	4,144	0	9	0
4	228	3	494	0	40	0
5	62	3	3	0	4	0
6	43	2	0	—	4	0
7	20	3	6	0	3	0
8	44	3	13	0	2	0
November 1965						
8	19	1	1	0	2	0
February 1966						
8	124	1	0	—	0	—
September 1966						
1	2	0	465	1	0	—
2	0	—	1,350	10	0	—
3	0	—	60	3	15	0
4	<50	1	130	5	18	1
5	272	0	43	0	12	1
6	1,346	12	382	0	159	0
February 1967						
6	21	1	6	0	0	—

specimens collected in sampling by the National Marine Fisheries Service (NMFS) in southeastern Alaska, south-central Alaska, the eastern Bering Sea, and the southeastern Chukchi Sea. Hoffman and Yancey (1966), who reported that *T. fagei* parasitized *Thysanoessa raschii* in Kachemak Bay, south-central Alaska, followed the development of external portions of the ellobiopsids from April through June. Examination of euphausiids collected during 4 yr (1962-66) of plankton sampling by NMFS in southeastern Alaska indicates that the ellobiopsids are most evident during May. Maturing ellobiopsids are seen on *T. raschii* as early as April and occasionally as late as December. A similar pattern of occurrence was described by Mauchline (1966) for *Thalassomyces fagei* on euphausiids in the North Atlantic.

Euphausia pacifica Hansen is abundant in lower Chatham Strait, southeastern Alaska, but is rarely parasitized by *T. fagei*. *Euphausia pacifica* bears this ellobiopsid off southern California (S. B. Collard, Marine Environmental Sciences Consortium, Dauphin Island, AL 36528, pers. commun.). An unidentified *Thalassomyces* was found on *E. pacifica* and *Thysanoessa longipes* Brandt in British Columbia (T. H. Butler, Biological Laboratory, Fisheries Research Board of Canada, Nanaimo, B.C., pers. commun.). In view of the wide distribution (Jones 1964) and known occurrence on at least 19 species of euphausiids (Vader 1973b), the British Columbia *Thalassomyces* is probably *fagei*. Komaki (1970) records *T. fagei* parasitizing *E. similis* G. O. Sars from Suruga Bay, Japan and *Thysanoessa inermis* (Krøyer) from the Bering Sea.

Thalassomyces capillosus (Fage 1938)

Amallocystis capillosus—McCauley (1962).
Thalassomyces capillosus—Collard (1966), Hoffman and Yancey (1966), Vader (1973a, b).

Thalassomyces capillosus is a parasite of the pelagic shrimp *Pasiphaea pacifica* from Coos Bay, Oreg., (McCauley 1962) to Prince William Sound, Alaska (Hoffman and Yancey 1966). I found nearly 700 *T. capillosus* in varying stages of development the year-round on *Pasiphaea* collected with a 1.8-m Isaacs-Kidd trawl in Chatham Strait and Lynn Canal. They were most abundant during the late spring and early summer, when it was not unusual to find 5 to 10% of the *Pasiphaea* in a sample parasitized; in one sample (May 1965 at the southern end of Chatham Strait) 47 of 115 *Pasiphaea* were parasitized by *T. capillosus*. *Thalassomyces capillosus* is also common in British Columbia (T. H. Butler, Biological Laboratory, Fisheries Research Board of Canada, Nanaimo, B.C., pers. commun.). Although *T. capillosus* are common in the northeastern Pacific, Vader (1973a) records only about

100 specimens in literature published on Atlantic *Pasiphaea* spp.

This parasite apparently has both physiological and morphological effects on the host shrimp. As noted by Bergan (1953), male and female shrimp were both parasitized; none of the parasitized females were carrying eggs, which indicates that the parasite must have sterilized the host. Although Bergan (1953) found no evidence that the root system of the parasite penetrates the host's gonads, it is possible that the parasite controls the sexual development and molting processes of the host either by influencing hormone production (Hoffman and Yancey 1966) or by a starvation effect (Wickstead 1963). In addition to the effect on growth and reproduction, *T. capillosus* causes a characteristic upward deflection of the host's rostrum (Boschma 1959; McCauley 1962; Hoffman and Yancey 1966). It is not known whether the deformation of the rostrum occurs before or after the primary stalks break through the cuticle of the host. The ellobiopsid is frequently lost or degenerates, but the upturned rostrum remains as evidence of parasitism. It was primarily on the basis of the upturned rostrum that *Pasiphaea principalis* Sund was erroneously distinguished from *P. tarda* Krøyer (Boschma 1959).

Thalassomyces californiensis Collard 1966

Thalassomyces californiensis n.sp.—Collard (1966).

Thalassomyces californiensis—Vader (1973a, b).

Thalassomyces californiensis is a parasite of the shrimp *Pasiphaea emarginata* Rathbun off the coast of central California (Collard 1966). *Thalassomyces californiensis* superficially resembles *T. capillosus*, but the primary stalks penetrate the eye stalks of the host rather than the base of the rostrum. Five to 20 primary stalks may be associated with each organ of fixation (Collard 1966) rather than the one to four primary stalks found in *T. capillosus*. Collard did not find any major morphological or histological changes caused by this parasite.

Thalassomyces species (not identified)

Thalassomyces sp.—Collard (1966).

A third species of *Thalassomyces* infects *Pasiphaea chacei* Yaldwyn in southern Baja California but is unidentified. This parasite is found on the anterior part of the abdomen (R. Lavenberg, Los Angeles County Museum of Natural History, Los Angeles, CA 90007, pers. commun.).

Ellobiopsis chattoni Caullery 1910

Ellobiopsis chattoni—Hoffman and Yancey (1966).

Hoffman and Yancey (1966) reported *E. chattoni* as a parasite of the calanoid copepod *Metridia longa* (Lubbock) in Auke Bay, southeastern Alaska. During monthly sampling of the Auke Bay vicinity by the NMFS from August 1962 to January 1964, copepods parasitized by *E. chattoni* were found from late July through December; 5 to 25% of the *M. longa* were parasitized and peak infestation was in late October and early November. Hoffman and Yancey (1966) found only *M. longa* infected by *E. chattoni* despite the availability of other potential calanoid hosts—*Calanus finmarchicus* (Gunnerus), *Pseudocalanus minutus* (Krøyer), and *Acartia clausii* Giesbrecht. Wickstead (1963) noted a similar 100% host specificity of *E. chattoni* on *Undinula vulgaris* var. *major* Sewell in the Zanzibar Channel.

There may be a large seasonal and yearly variation in the rate of infection by ellobiopsids and perhaps even in the species of copepod infected. I sampled zooplankton monthly in Auke Bay and near Point Retreat (Figure 5) from September 1969 through October 1970. During this time, *E. chattoni* did not infect *M. longa* but did infect *P. minutus*; the level of infection was very low, however: one to six *P. minutus* were taken each month from the thousands of potential hosts examined, but no distinct seasonal trend of infection was evident.

Ellobiocystis caridarum (Coutiere 1911)

Sampling with the 1.8-m Isaacs-Kidd mid-water trawl in southeastern Alaska yielded many *Pasiphaea pacifica* (a pelagic shrimp) with the epibiont *E. caridarum* on their mouth parts. Boschma (1959) discussed the difficulties in identifying the various species of *Ellobiocystis*

described by Coutiere. Boschma also examined the question of including the genus *Ellobiocystis* within the family Ellobiopsidae and of including various epibionts described by With (1915), Monod (1926), and Sewell (1951) within the genus. I follow Boschma (1959) in considering the *Ellobiocystis* found on *P. pacifica* to belong to the collective species *E. caridarum* s.l. This constitutes the first record of *E. caridarum* s.l. outside of the Atlantic and Antarctic oceans.

Ellobiocystis caridarum attach as single trophomeres directly to the mouth parts of the host. There is no branching of the trophomeres, and no organs of adsorption penetrate the cuticle of the host. The trophomeres may occur singly or in small groups attached to the labia, mandibles, maxillae, or maxillipeds. Single trophomeres on the oral appendages are usually attached near the base of a seta, sometimes directly to a seta. When on the mandibles, the trophomeres are located between the teeth. Groups of trophomeres, each trophomere separately attached to the host's cuticle, may contain 12 or more individuals when on the labia but usually contain less than 8 when attached to the maxilla or maxillipeds. I have seen nearly 50 *E. caridarum* on a single *Pasiphaea*.

The size and form of *E. caridarum* s.l. found on *P. pacifica* in southeastern Alaska are as variable as the size and form figured by Boschma (1959) for the *E. caridarum* found on *P. semispinosa* Holthuis. The maximum observed length of trophomeres of Alaska specimens was 1.17 mm and of gonomeres was 0.54 mm; the maximum diameter of trophomeres was 0.56 mm and of gonomeres was 0.42 mm. The shapes of the gonomeres varied from ovals, slightly longer than wide, to rods eight times longer than wide. Each maturing trophomere carried one gonomere; less than 1% of the trophomeres had two or three gonomeres.

The incidence of *E. caridarum* s.l. on *P. pacifica* is not known, primarily because the epibiont is not readily noticeable in either the living or preserved state. When searched for, *E. caridarum* have been found on *P. pacifica* of a wide size range (30 to 80 mm total length) and during all months of the year. The proportion of the *P. pacifica* having *E. caridarum* varies but is usually less than 10%. In one exceptional sample (AB65-15, southern Chatham Strait, May 1965), 84% (263 of 314) were infested.

Ellobiocystis species?

Monod (1926) figured an epibiont found on the mouth parts of the Antarctic amphipod *Podocerus septemcarinatus* Shellenberg (= *Platophium hystricoides* Monod). This epibiont has been provisionally classified as *Ellobiocystis caridarum* by Boschma (1959). Vader and Kane (1968) reported a similar epibiont on the mouth parts of *Rhachotropis macropus* from western Norway. The taxonomic status of these epibionts still is uncertain (W. Vader, Zoologisk Avdeling, Tromsø Museum, Tromsø, Norway, pers. commun.).

I found small epibionts like those figured by Monod (1926) on the amphipod *R. helleri* from Auke Bay, Alaska. The small bean-shaped organisms (Figure 6) are attached to the labia, mandibles, and maxillipeds of the host by a short stalk. Lengths range from 0.10 to 0.13 mm. The separation of body and stalk is more distinct than in the *E. caridarum* figured by Boschma (1959) or than in material from *Pasiphaea pacifica* that I have seen. None of the epibionts on *R. helleri* are divided into gonomeres or spores. Although these epibionts superficially resemble early stages of developing *E. caridarum*, their proper identification remains in doubt.

SUMMARY

1. *Thalassomyces boschmai* is found on the mysids of the genera *Acanthomysis, Neomysis*, and *Meterythrops* in the northeastern Pacific.

2. *Thalassomyces albatrossi* n.sp. is described as a parasite of *Stilomysis major* from the western Pacific off Korea.

3. *Thalassomyces fasciatus* is found on *Gnathophausia ingens* and *G. gracilis* from Baja California and southern California.

4. *Thalassomyces marsupii* is found on the amphipods *Parathemisto pacifica, P. libellula*, and *Cyphocaris challengeri* from the inside coastal waters of southeastern Alaska and *P. pacifica* from Puget Sound.

5. *Thalassomyces fagei* has been found on the euphausiid *Thysanoessa raschii* from southeastern Alaska, the Bering Sea, and the Chukchi Sea and on *Euphausia pacifica* from California and southeastern Alaska.

6. *Thalassomyces capillosus* is common on the shrimp *Pasiphaea pacifica* in the coastal waters

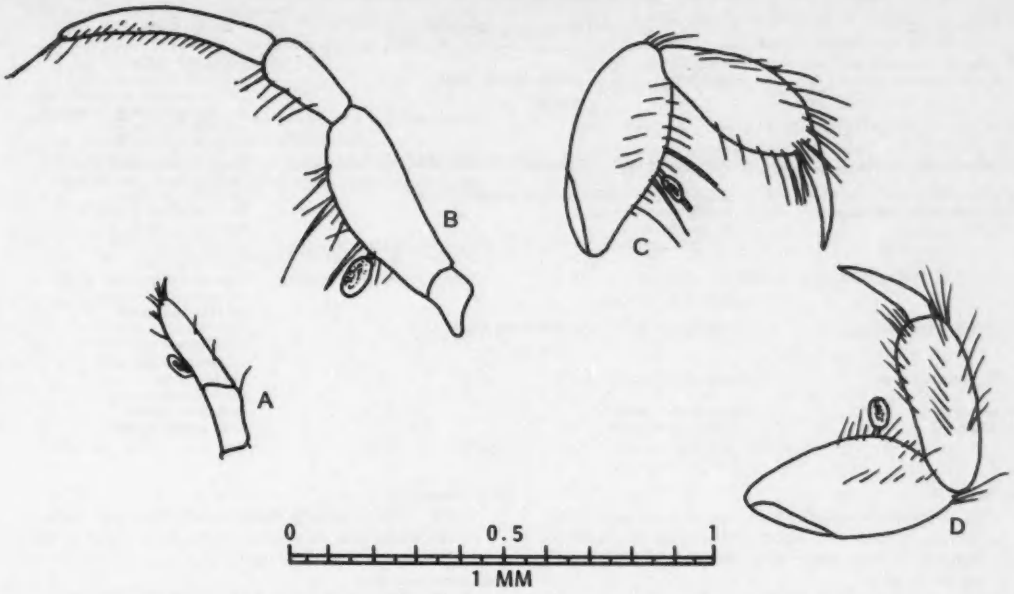

FIGURE 6.—*Ellobiocystis* sp.? on mouth parts of the amphipod *Rhachotropis helleri*. A. Palp of first maxilla. B. Mandibular palp. C. and D. Maxilliped palps.

of the northeastern Pacific during all seasons of the year.

7. *Thalassomyces californiensis* is found on *P. emarginata* from southern California.

8. *Ellobiopsis chattoni* is found on the copepod *Metridia longa* from Auke Bay, Alaska, from July through December; peak abundance is in late October and early November. *Pseudocalanus minutus* is also a host of *E. chattoni*.

9. *Ellobiocystis caridarum* is found in a wide variety of growth forms on *Pasiphaea pacifica* from southeastern Alaska during all seasons of the year. Incidence of infestation by *E. caridarum* may be as high as 84% of the *Pasiphaea*. This is the first report of *E. caridarum* from the North Pacific.

10. A small epibiont resembling *E. caridarum* has been found on the mouth parts of the amphipod *Rhachotropis helleri* from Auke Bay, Alaska.

11. Known North Pacific ellobiopsids, their hosts, and the geographical range of the ellobiopsids are summarized in Table 6.

ACKNOWLEDGMENTS

I wish to express my gratitude to T. H. Bowman of the U.S. National Museum for the loan of the holotype of *Thalassomyces albatrossi* n.sp. and identification of the amphipods and mysids found as hosts of *Thalassomyces* spp. Correspondence with S. B. Collard of the University of West Florida and W. Vader of Tromsø, Norway has been most informative as were discussions with Ethelwyn Hoffman in the early stages of the study. Thanks are due also to J. Galt of the University of Washington; T. H. Butler of the Fisheries Research Board of Canada; and R. A. McHardy of Southampton, England, for information on recent host and range extensions of several ellobiopsid species. R. E. Thorne kindly supplied specimens from his Puget Sound plankton collections. J. Campbell, Language Department, University of Rhode Island, translated the species diagnosis into Latin.

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TABLE 6.—North Pacific ellobiopsids, known North Pacific range, and known North Pacific hosts.

Ellobiopsid	Known North Pacific range of ellobiopsid	Known North Pacific hosts
Thalassomyces albatrossi n.sp.	Eastern Korea	*Stilomysis major*
Thalassomyces boschmai	Puget Sound, Wash., to Kachemak Bay, Alaska	*Acanthomysis macropsis* *Acanthomysis pseudomacropsis* *Acanthomysis nephrophthalma* *Neomysis kadiakensis* *Meterythrops robusta*
Thalassomyces fasciatus	Southern Baja California to Santa Cruz Basin, Calif.	*Gnathophausia gracilis* *Gnathophausia ingens*
Thalassomyces capillosus	Southern Oregon to Prince William Sound, Alaska	*Pasiphaea pacifica*
Thalassomyces californiensis	Central California	*Pasiphaea emarginata*
Thalassomyces sp.	Baja California	*Pasiphaea chacei*
Thalassomyces fagei	Southern California to southeastern Chukchi Sea; Suruga Bay, Japan	*Euphausia pacifica* *Euphausia similis* *Thysanoessa inermis* *Thysanoessa longipes* *Thysanoessa raschii*
Thalassomyces marsupii	Puget Sound, Wash., to southeastern Alaska	*Parathemisto pacifica* *Parathemisto libellula* *Cyphocaris challengeri*
Ellobiopsis chattoni	Southeastern Alaska	*Metridia longa* *Pseudocalanus minutus*
Ellobiocystis caridarum	Southeastern Alaska	*Pasiphaea pacifica*
Ellobiocystis sp.	Southeastern Alaska	*Rhachotropis helleri*

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A DESCRIPTION OF ATLANTIC MACKEREL, *SCOMBER SCOMBRUS*, EGGS AND EARLY LARVAE

PETER L. BERRIEN[1]

ABSTRACT

The development of laboratory-reared Atlantic mackerel, *Scomber scombrus*, eggs and early larvae is described in order to augment published descriptions of this species. The eggs are spherical, have a diameter of 1.01 to 1.28 mm, and have a single, yellowish oil globule, 0.22 to 0.38 mm in diameter. Melanophores, first visible after blastopore closure, assume a distinct pattern on the embryo. Melanophores are present on the oil globule but are absent from the yolk surface except immediately prior to hatching. Hatching occurs at 90 to 102 h after fertilization at an average incubation temperature of 13.8°C. Bodily pigmentation of the larvae undergoes considerable change during yolk absorption; eye pigmentation is apparent at 66 h after hatching. The yolk is fully absorbed by 137 h after hatching, and teeth are present in 192-h-old larvae.

To complement ichthyoplankton survey work underway at the Sandy Hook Laboratory, eggs of a few fish species have been artificially spawned and reared in the laboratory. These series of known identities were obtained for comparison with eggs and larvae from plankton samples. The purpose of this paper is to present descriptive information on the eggs and early larvae of Atlantic mackerel, *Scomber scombrus* Linnaeus 1758, and, in so doing, to augment previous descriptions of the young stages of this species, particularly of the eggs.

Previous publications containing helpful information on identification of North American Atlantic mackerel eggs and larvae are by Sette (1943), who included descriptive notes on eggs and larvae and compared them with young stages of other species present in the same waters, and by Bigelow and Schroeder (1953), who presented a brief egg and larval description and illustrated four larval stages. Other, less helpful, descriptive notes on North American Atlantic mackerel eggs and larvae are by Moore (1899), Dannevig (1919), Bigelow and Welsh (1925), Sparks (1929), Merriman and Sclar (1952), Wheatland (1956), and Marak and Colton (1961). Worley (1933) described the rate of embryonic development of Atlantic mackerel at various temperatures. Other papers describing eggs and larvae of Atlantic mackerel, probably of a separate European race (Garstang 1897-99), include Cunningham (1891-92a, b), Ehrenbaum (1905-09), Bigelow and Welsh (1925), Sella and Ciacchi (1925), and Padoa (1956). However, adequate descriptions of Atlantic mackerel eggs are lacking in the literature because descriptive information by most of the above authors is limited to reports of egg and oil globule diameters. Illustrations, where presented, are of little use in differentiating this from other species. The reported egg dimensions vary greatly and overlap those of other species present at the same time and in some of the same areas as Atlantic mackerel. Regarding this problem, Sette (1943) described a technique of plotting oil globule diameter against egg diameter for all eggs in hauls containing troublesome mixtures. In these scatter diagrams the Atlantic mackerel eggs remained discrete from other species' eggs.

The congeneric chub mackerel, *Pneumatophorus diego* (= *Scomber japonicus*) eggs and larvae from the eastern Pacific Ocean were described by Fry (1936), Orton (1953), and Kramer (1960) and from the western Pacific Ocean by Uchida et al. (1958), Dekhnik (1959), and Watanabe (1970). The papers by Orton, Kramer, and Watanabe contain very detailed and useful descriptions. Eggs and yolk-sac larvae of *S. scombrus* and *S. japonicus*, judged by my specimens and the above-mentioned descriptions, are similar, but differ in that: *S. japonicus* late-stage eggs and early yolk-sac lar-

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vae have more melanophores on the yolk surface than *S. scombrus*; and *S. scombrus* larvae, during and at the end of yolk absorption have several dorsal trunk melanophores, whereas few *S. japonicus* at this stage have any such pigmentation. In those *S. japonicus* which have dorsal melanophores on the trunk, it is apparently limited to a single patch near the 23rd myomere (Fry 1936; Uchida et al. 1958; Kramer 1960). Separation of the two species of *Scomber* early-stage eggs, before blastopore closure, may be impossible on the basis of morphological characters. Other factors, such as spawning time and area, and the proximity of older, identifiable stages, may be necessary for subjective identifications.

PROCEDURES

Running ripe Atlantic mackerel were caught by hook and line off Fire Island, Long Island, N.Y., during the morning of 2 June 1967. Several hundred eggs were stripped from one female and fertilized in a liter jar containing a small amount of seawater. The water was renewed about 20 min after introduction of the eggs and sperm, and the jar placed in a water bath to minimize temperature changes. The water temperature generally increased during egg incubation and larval life and ranged from 12.1° to 14.4°C for eggs and from 14.1° to 15.2°C for larvae (Table 1). Larvae were not fed and none survived longer than 8 days past hatching. Samples of the developing eggs and larvae were removed at intervals and preserved in dilute Formalin.[2]

While the following descriptions of eggs were based mainly on cultured eggs, planktonic eggs were utilized in obtaining dimensions (Table 2) and in confirming pigmentation, which tended to be faded and obscure in the cultured specimens. Owing to the internally damaged condition of early-stage eggs from plankton samples only middle- and late-stage eggs from that source were used for the above purposes. In the early-stage eggs the yolk and oil globule membranes ruptured and allowed the yolk and fractured oil globule to mix with perivitelline fluid. Planktonic eggs were taken by Gulf V high-speed samplers, with 0.4-m mouth and 0.52-mm mesh openings.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Dimensions of Atlantic mackerel larvae, cultured series.

Hours from hatching	Number of larvae	Culture temp. (°C)	Standard length (mm)		Total length (mm)	
			Mean	Range	Mean	Range
0	3	14.1	3.25	3.03-3.36	3.39	3.16-3.50
6	10	14.1	3.47	3.30-3.58	3.62	3.47-3.75
18	7	14.1	3.59	3.44-3.70	3.76	3.61-3.84
42	8	14.4	3.77	3.67-3.84	3.99	3.89-4.05
66	3	14.6	3.85	3.78-3.94	4.08	4.00-4.16
137	7	15.2	3.92	3.84-4.03	4.14	4.05-4.19
166	3	15.1	4.02	3.81-4.25	4.24	4.03-4.47
192	2	14.8	3.97	3.75-4.19	4.21	3.97-4.45

The samples were taken in step-oblique tows at depths between 0 and 33 m, at a speed of 5.0 knots.

DESCRIPTION OF THE EGG

Dimensions

Formalin-preserved Atlantic mackerel eggs are spherical and have clear and unsculptured shells (Figure 1). The mean diameter of eggs from plankton samples is 1.13 mm (range 1.01 to 1.28 mm) and of those that were cultured is 1.20 mm (range 1.13 to 1.25 mm, Table 2). The cultured eggs were stripped from a single female, while those from plankton samples undoubtedly were spawned by many. This may account for the smaller range in egg diameter from the cultured series and the difference in mean diameters from the two sources. Differential shrinkage of egg diameter, due to varying time in preservation, between cultured and planktonic eggs is assumed negligible, as all eggs were measured more than a year after preservation.

The egg contains a single oil globule which is generally spherical and yellow or pale amber. Its diameter ranges from 0.22 to 0.38 mm, with a mean for all samples of 0.29 mm (Table 2). In many of our preserved samples, from both the cultured and planktonic eggs, the oil globules were fractured or distorted. The dimensions presented here lie within the range of those given by previous authors who have studied Atlantic mackerel. Published observations on eggs of this species from western North Atlantic waters report a range in egg diameter of 0.88 to 1.38 mm, with mean or modal values of 1.15 to 1.30 mm, and an oil globule diameter of 0.24 to 0.32 mm (Moore 1899; Dannevig 1919; Bigelow and Welsh 1925; Sparks 1929; Sette 1943; Merriman and Sclar 1952; Wheatland 1956; Marak and Colton 1961).

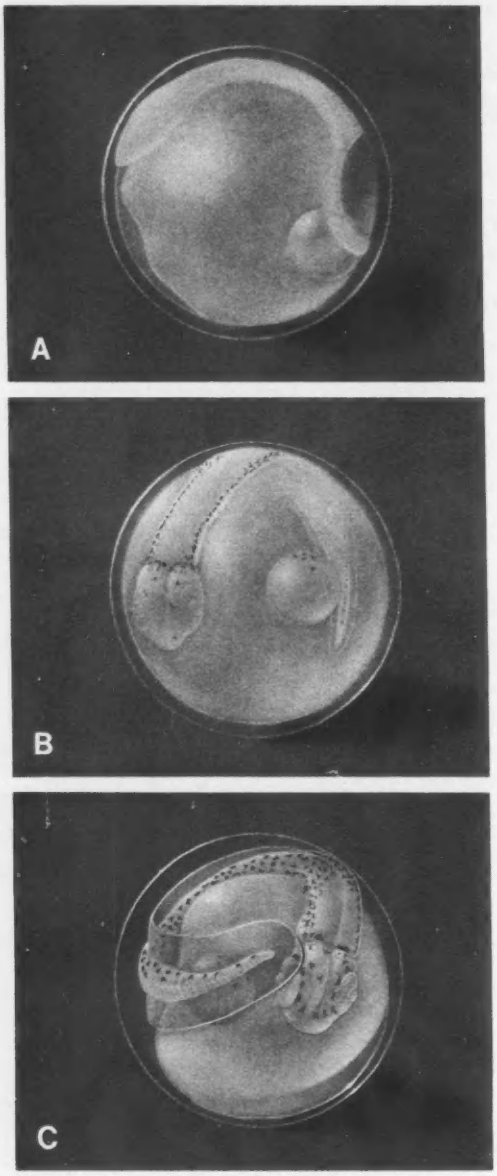

FIGURE 1.—Atlantic mackerel eggs: A, early stages; B, middle stage; C, late stage.

Perivitelline Space

In live eggs, the perivitelline space occupies about one-twentieth of the eggshell diameter, or about 0.05 mm. The eggs illustrated (Figure 1) are idealized only to the extent that the width of perivitelline space conforms to the observations on live eggs.

Pigmentation

Two large yellow chromatophores were observed in the live eggs at 60 and 85 h after fertilization. These chromatophores were situated on either side of the embryo immediately behind the head. No further notes on chromatophores of this color were kept. By the time I observed the eggs and larvae, several months after preservation, only melanophores were observed. All further comments on pigmentation refer to melanophores.

Development

Following the criteria of Ahlstrom and Ball (1954), this paper describes the development of the Atlantic mackerel egg in three stages: early (fertilization to closure of the blastopore), middle (blastopore closure to the twisting of the tail), and late (tail twisting to hatching). The early stage terminated shortly after 36 h, as the blastopore was 0.3 mm across at that time; the middle stage was completed by 72 h, when the tail was observed twisted; and the late stage lasted till hatching, by 102 h after fertilization. Incubation temperature ranges of the three stages were: early, 12.1° to 14.4°C; middle, 13.8° to 14.2°C; and late, 14.1° to 14.2°C.

Early-Stage Eggs (Figure 1A)

Early-stage Atlantic mackerel eggs are characterized by the dimensions given above and by the presence of a single yellow oil globule. The oil globule is off-center at the vegetal pole, opposite the blastodisc at first and, with development of the embryo, slightly posterior to the tail at the time of blastopore closure. There are no visible myomeres, pigmentation, or formed eyes.

Middle-Stage Eggs (Figure 1B)

Soon after the blastopore closes, pigmentation becomes visible on the embryo as numerous, scattered fine points on the dorsal surface of the thoracic region and a few back along the trunk.

TABLE 2.—Dimensions of Atlantic mackerel eggs from the cultured series and plankton samples taken during May and June 1966.

Item	Egg diameter (mm)			Oil globule diameter (mm)		
	No.[1]	Mean	Range	No.[1]	Mean	Range
Cultured series:						
Early stage	537	1.19	1.13-1.25	371	0.29	0.24-0.36
Middle stage	43	1.20	1.17-1.24	36	0.32	0.27-0.36
Late stage	42	1.20	1.16-1.22	42	0.32	0.28-0.33
Total cultured	622	1.20	1.13-1.25	449	0.30	0.24-0.36
Plankton samples, middle- and late-stage eggs:						
19 May 1966						
38°01.5'N, 74°59.0'W	54	1.18	1.06-1.28	53	0.32	0.27-0.38
17 June 1966						
41°17.0'N, 70°48.0'W	163	1.14	1.01-1.27	156	0.28	0.22-0.35
41°12.0'N, 70°47.0'W	114	1.12	1.02-1.26	113	0.31	0.24-0.38
41°07'N, 70°46.0'W	62	1.08	1.02-1.21	62	0.28	0.22-0.32
Total plankton	393	1.13	1.01-1.28	384	0.29	0.22-0.38

[1]Discrepancies between numbers of specimens in these columns are due to fractured or distorted oil globules, which were not measured.

As development progresses, these pigment cells become more intense and increase in number on the trunk where they tend to line up in two dorsolateral rows. The lateral melanophores in the thoracic region become dendritic and dense, while the middorsal melanophores fade. This distinct thoracic pattern persists until hatching. Melanophores appear on the anterior surface of the oil globule at the same time as those on the embryo.

The width of the head increases to almost twice that of the tail. The embryo increases in length, growing past the oil globule and encircling three-fourths of the egg by the end of this stage. The tail twists and flexes near the oil globule until it lies flat against the yolk surface. A finfold begins to develop on the posterior one-third of the embryo. Optic vesicles become prominent and up to six myomeres are discernible.

Late-Stage Eggs (Figure 1C)

At the start of the late stage, there are two dorsolateral rows of melanophores extending back from just behind the brain, well past the oil globule; there are few melanophores below these rows on the flanks. There is always pigment on the anterior half of the oil globule, and usually some on the snout and in a row behind the eyes across the head. During this stage, trunk melanophores migrate; they become scattered on the flanks and in some specimens a few melanophores posterior to the oil globule nearly reach the ventral edge of the body by the time of hatching. Pigment is lacking on the extreme caudal portion of the body. Melanophores on the oil globule darken and increase in number and coverage, so that just before hatching they are scattered over most of the oil globule. As many as 24 myomeres are visible prior to hatching. The dorsal line of melanophores behind the eyes persists on most embryos. The eyes are unpigmented through hatching.

The embryo increases in length until it encircles the yolk, with the tail overlapping the head just before hatching. The oil globule lies midway along the body, at the posterior end of the yolk sac, at hatching. The finfold deepens and extends forward to occupy the posterior two-thirds of the embryo. Before hatching the alimentary tract is visible posterior to the oil globule and terminates at the edge of the ventral finfold.

DESCRIPTION OF LARVAE

Rate of Development

Hatching occurred between 90 and 102 h after fertilization at an average incubation temperature of 13.8°C (range 12.1° to 14.4°C). This was a slightly faster rate of development than that reported by Worley (1933). At this temperature (13.8°C), interpolation of Worley's data would indicate a time to hatching of about 120 h. The yolk-sac stage ended by 137 h, for the yolk in all specimens was absorbed by that time.

Pigmentation at Hatching (Figure 2A)

Melanophores are distributed as follows: some tend to be in dorsolateral rows, extending on each side from the snout over the eyes to about nine-tenths of the body length, while others are

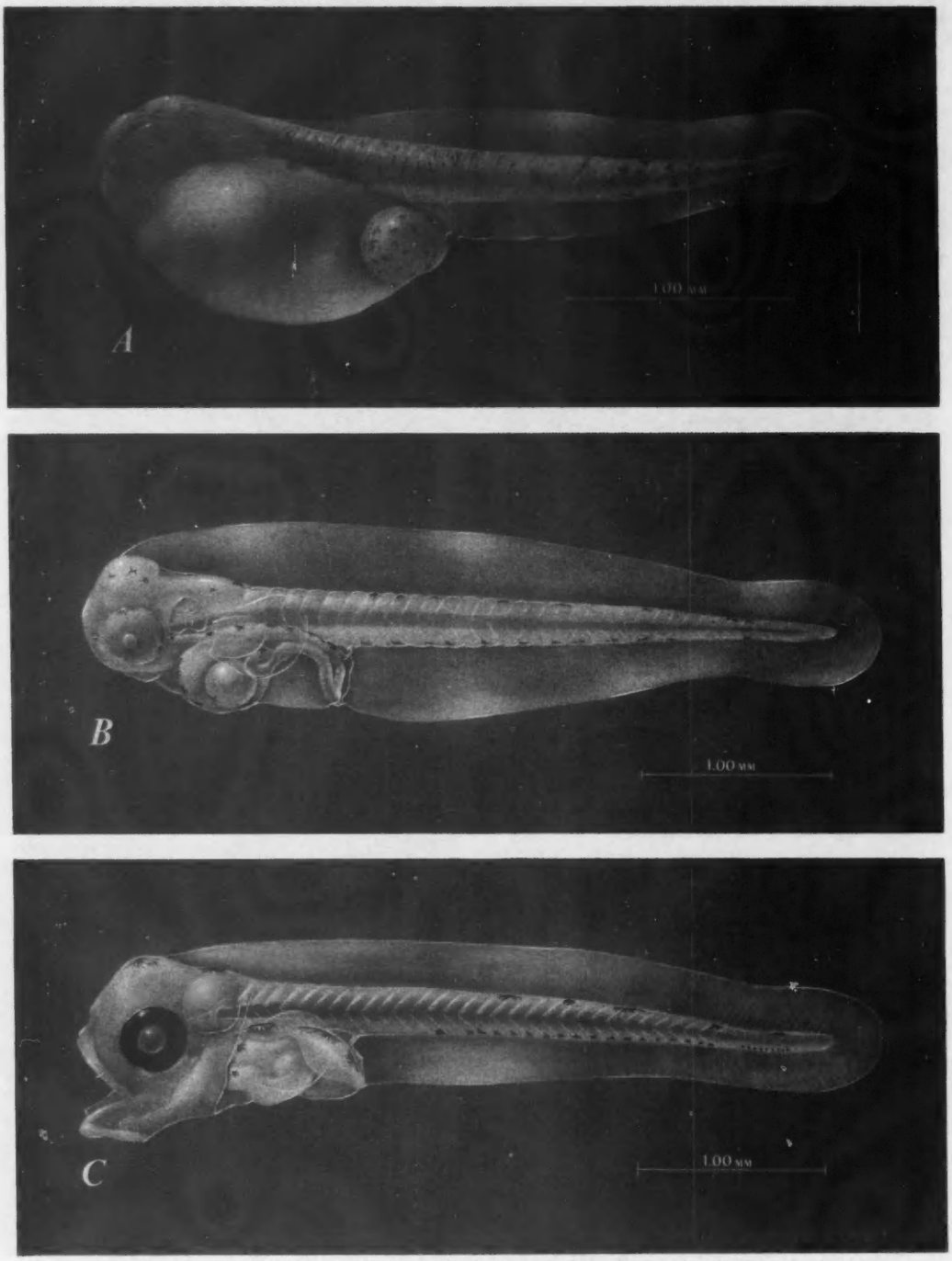

FIGURE 2.—Atlantic mackerel larvae: A, shortly after hatching; B, 66 h after hatching; C, 192 h after hatching.

scattered on the flanks; they are found on the nape; one on each side of the yolk-sac close to the otocysts; and scattered on the oil globule.

Subsequent yolk-sac stages undergo marked pigmentation changes, including the migration and formation, or initial appearance of melanophores. Orton (1953) reported similar melanophore migration in *Pneumatophorus japonicus diego* (= *S. japonicus*) eggs and yolk-sac larvae.

Head Pigmentation

Pigment on the head becomes reduced to a few melanophores dorsal to the eyes and on the nape (Figure 2B, C). At 66 h, pigment forms in the eyes. Some specimens, between 137 and 192 h, have a melanophore on the ventral midline between the developing dentaries where the basihyal forms.

Abdominal Pigmentation

Melanophores present on the oil globule at hatching and at 6 h start migrating to the ventral surface of the yolk sac by 18 h, and are mostly on that surface by 42 h. Subsequently, these melanophores tend to coalesce on two areas: on the forward end of the gut cavity between the cleithra (Figure 2B, C) and, in some specimens, on the ventral surface of the hindgut. This pigmented area on the hindgut varies in occurrence, intensity, and location.

At 18 h, some of the melanophores which were on the sides of newly hatched larvae, above the middle of the yolk sac, are migrating ventrally and inward above the yolk mass. By 66 h, this pigment is situated over the dorsum of the midgut and hindgut. Older specimens, up to 192 h, all have intense or large dendritic melanophores directly above the gut cavity (Figure 2C).

Caudal Pigmentation

The two dorsolateral rows of melanophores, already somewhat scattered on the flanks at hatching (Figure 2A), migrate toward the bases of the dorsal and anal finfolds; this condition is complete by 66 h (Figure 2B). Those melanophores at the dorsal finfold base decrease to about 6 by 192 h and are located on the posterior half of the larva; those in the ventral row increase to about 20 to 25 and extend from near the vent back to the caudal extremity, exclusive of finfold.

Myomeres

At 102 h, only 23 or 24 myomeres were observed in the unhatched eggs. Others most certainly present were obscured by the opacity of the yolk. In the newly hatched larvae, however, the full complement of 31 myomeres was evident.

Finfold

In newly hatched larvae, a continuous finfold extends posteriorly on the dorsal surface from slightly behind the auditory vesicle, around the caudal extreme, then forward on the ventral surface to the yolk sac. The finfold broadens, lengthens, and reaches the top of the head by 66 h where it persists to 192 h. With development, the ventral finfold extends forward to the anus, and as the yolk sac decreases in length the preanal finfold occupies the area between the anus and yolk sac. Actinotrichia are barely visible in the caudal portion of the finfold on newly hatched larvae and become more evident on older stages (Figure 2).

Alimentary Canal

The hindgut, observable in the ventral finfold of larvae at hatching as a narrow tract, is much thickened at 18 h. Mouth rudiments are present on 66-h larvae, and by 137 h, when the yolk material is completely absorbed, the mouth is open. A pair of recurved teeth occur on each jaw at 192 h (Figure 2C).

Otocysts

The otocysts are visible at hatching. Developing otoliths are barely visible at 42 h and are plainly evident by 66 h (Figure 2).

Pectoral Buds

The newly hatched larvae have pectoral buds. By 66 h, these buds have fleshy bases, fan-shape membranes, and appear functional (Figure 2A, B).

SUMMARY

For identification purposes, it is useful to summarize some of the more prominent features of Atlantic mackerel eggs and early larvae. The

egg has an average diameter of 1.08 to 1.20 mm, and contains a single, yellowish oil globule averaging 0.28 to 0.32 mm in diameter. A distinctive pigment pattern forms on the embryo after the blastopore closes. The eyes remain unpigmented through hatching.

Pigmentation on the larvae undergoes considerable change during the yolk-sac stage. Newly hatched larvae have scattered melanophores on the dorsal and lateral surfaces of the head and trunk and on the oil globule. By the time the yolk is used up, pigment coalesces onto the dorsal and ventral surfaces of the trunk, above the brain and gut, and forms in the eyes. Teeth are present in 192-h-old larvae, at a size of 4.0 mm standard length.

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THE CONCENTRATION OF MERCURY, COPPER, NICKEL, SILVER, CADMIUM, AND LEAD IN THE NORTHERN ADRIATIC ANCHOVY, *ENGRAULIS ENCRASICHOLUS*, AND SARDINE, *SARDINA PILCHARDUS*

MALVERN GILMARTIN[1] AND NOELIA REVELANTE[2]

ABSTRACT

Levels of mercury, copper, nickel, silver, cadmium, and lead were determined in various tissues of the northern Adriatic anchovy, *Engraulis encrasicholus*, and sardine, *Sardina pilchardus*, throughout a 7-month fishing season. The highest concentrations of nickel, silver, cadmium, and lead occurred in the skin and gills, with little interspecific differences and no unusually high values. The highest concentrations of mercury and copper occurred in internal tissues, with the anchovy showing markedly higher concentrations than the sardine. Total mercury concentrations in anchovy muscle ranged from 70 to 215 nanograms per gram wet weight, concentrations 2-4× greater than in the same or similar anchovy species off northwestern Africa, southeastern United States, and California.

The Adriatic Sea extends 800 km into the heartland of the European continent, and is bordered by Italy, Yugoslavia, and Albania. The extended coastal shelf of the northern portion is an important fishery region, exploited heavily by both Italy and Yugoslavia.

Unfortunately, with restricted exchange to the open Mediterranean, the Adriatic displays many of the characteristics of a narrow trapped sea. Furthermore, the shallow northern region receives industrial wastes disproportionate to its area from large industrial centers located along the eastern coast at Rijeka and Pula, Yugoslavia, and more extensive industrial concentrations on the Gulf of Trieste and the western coast near Venice, Italy. More significantly, the Reno, Po, Adige, and Isonzo rivers discharge their industrial pollutant loads into the northern Adriatic. The Po alone is the second largest and perhaps most heavily polluted river entering the entire Mediterranean, and has a drainage area more than three-quarters the total area of the Adriatic itself. In 1972, 76 plants were discharging their waste water directly or indirectly into the Venice lagoon, and 10,000 of the 64,000 hectares of the lagoon were considered seriously polluted. Consequently, it is estimated that about 70% of the total organic load of industrial waste entering the Adriatic Sea from the west is concentrated in the northern part of the sea (General Fisheries Council for the Mediterranean 1972).

In contrast, although the deeply indented eastern coast has more than twice the shoreline of the western coast, population density and industrialization are markedly lower, and no major rivers flow into the Adriatic from the east. However, the level of industrialization and population density is increasing on both coasts of the Adriatic, and already the level of some heavy metals (e.g. mercury) in water and edible marine organisms in the open Adriatic may be at, or even slightly above, the acceptable safety level (General Fisheries Council for the Mediterranean 1972).

Recent research has drawn attention to the increasing hazards of heavy metal pollution in the marine environment (Ruivo 1972). Continental shelf fisheries, such as those of the shallow northern Adriatic, are especially threatened by these materials since large amounts can be introduced into restricted areas by coastal waste water runoff and the fallout of aerosols.

Therefore, a preliminary survey of the levels of mercury and copper, and the potentially toxic metals nickel, silver, cadmium, and lead in the sardine *Sardina pilchardus* Walbaum and the

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anchovy *Engraulis encrasicholus* Linnaeus was conducted during 1972 and 1973 to establish currently occurring levels of these elements and to produce a baseline for future reference.

The Fishery

The total fish catch landed in the eastern Adriatic remained relatively stable from 1964 through 1971, at 25,000-30,000 metric tons (Food and Agriculture Organization of the United Nations 1972), with an additional 2,000-3,000 metric tons taken annually for noncommercial use. Three small pelagic species of clupeids consistently compose at least 70% of this catch (Table 1), about 85% of which is canned, the balance being sold fresh. No significant fish meal industry currently utilizes these species.

There is strong evidence that the sardine is already fished to capacity, but that the anchovy may be significantly underexploited (Major 1970). The two species selected for the initial survey were the sardine, the most abundant and commercially most important species in the Adriatic, and the anchovy, the species suspected of having the greatest potential for increased production.

The Stock

The population structure and migration patterns of the Adriatic sardine and anchovy are not well understood. Gamulin (1956) opined that the sardine population migrates offshore annually from the very shallow waters of the northern Adriatic to somewhat deeper waters (60-120 m), but not into the central Adriatic, a behavior pattern typical of the species (Larrañeta 1960). Zavodnik (1968) presented similar evidence, noting that the species is completely absent from the shallow coastal zone by December. Krajnović and Dekaris (1968) found serological evidence that various subpopulations pass the Istrian coast during these migrations.

Evidence for anchovy migrations, e.g. based on seasonal variations in catch statistics at various ports, appears somewhat clearer. Piccinetti (1970) suggests that the population "winters" off Ancona and farther south off the western coast of the Adriatic, and during the spring migrates eastward and then northward along the Dalmatian coast, reaching the Istrian islands and peninsula during early summer. Continuing into the Gulf of Trieste and westward to Venice during autumn, the population returns to its "wintering" grounds by December.

While it is difficult to define exact migratory routes, or to delimit subpopulations, the evidence suggests that a composite stock of sardine and anchovy exists in the northern Adriatic, and that the Rovinj fishery "samples" much of this stock as it migrates past the Yugoslav Istrian peninsula.

MATERIALS AND METHODS

Sampling

During 1972 the major fishing season off Istria extended from June to December, rather than the more common May to October season. Samples were collected throughout the 1972 season and during the first few months of the 1973 season from the catch landed at the Mirna Cannery in Rovinj, Yugoslavia. These fish were usually caught within the preceding 12-18 h, within 15-30 km of Rovinj, using night light and purse seine.

Each sample usually consisted of at least six "representative" sardines and six "representative" anchovies selected from the catch, although often 50, and occasionally up to 60, fish were collected. Samples were immediately taken to

TABLE 1.—Yugoslavia's marine fisheries catch, 1964-71.

Species[1]	Nominal catch in thousands of metric tons							
	1964	1965	1966	1967	1968	1969	1970	1971
Sardina pilchardus (sardine)	5.4	9.4	9.1	11.2	13.5	13.5	10.9	14.7
Clupea sprattus (sprat)	5.0	5.7	3.4	2.5	3.2	2.0	5.5	3.8
Engraulis enchrasicholus (anchovy)	4.9	2.2	4.8	7.3	4.8	4.0	3.0	3.1
Scomber scombrus (Atlantic mackerel)	2.6	0.8	2.3	1.2	1.1	0.5	0.3	0.1
Boops boops (greater amberjack)	1.3	0.7	1.4	1.4	1.4	1.3	1.1	1.0
Maena maena, M. smaris (mullet)	1.3	1.1	1.0	1.0	0.9	0.8	0.7	0.3
Misc. marine fishes (18 spp.), Crustacea, and Mollusca	4.8	6.1	5.3	5.4	5.0	4.8	4.1	7.8
Total marine catch	25.3	26.0	27.3	30.0	29.9	26.9	25.6	30.8

[1]All scientific and common names from Bini (1965).

the Center for Marine Research in Rovinj, weighed and their standard length determined. Each fish was then dissected into component parts, e.g. skin (including scales), gills, muscle. These components were then pooled according to type, weighed, dried to a constant weight at 110°C, ground to homogeneous meal in a porcelain mortar, and stored in a glass desiccator until analyzed.

Analytical Methods

Standard chemical procedures (Christian and Feldman 1970; Fletcher 1970; Uthe et al. 1970; Stainton 1971) as modified by Knauer and Martin (1972) were used. For all elements except mercury, two 1-g aliquots of sample plus 10 ml 70% redistilled HNO_3 were added to 30-ml beakers, which were covered with watch glasses and refluxed at 90°C for 2 h, followed by evaporation to dryness. After charring, the samples were redissolved in 5 ml 70% HNO_3, followed by the dropwise addition of 30% H_2O_2 until the samples remained clear. At this point the samples were evaporated to 5 ml, cooled, and diluted to 25 ml with distilled water.

All samples were analyzed on a Perkin-Elmer 303 atomic absorption spectrophotometer.[3] Various combinations of fuels and oxidants, as recommended in the Perkin-Elmer manual, were used for each element. Small differences between signal and base line in some of the Cd, Ni, and Ag analyses may have introduced error.

Procedures for mercury differed slightly. Approximately 0.2-0.4 g dry weight of sardine and anchovy tissues were weighed into 20-ml Neutraglas disposable ampoules, followed by the addition of 3 ml of a 2:1 solution of concentrated H_2SO_4 and HNO_3. Samples were heated on a hotplate overnight at 80°C, cooled in ice, followed by the addition of 8 ml 6% $KMnO_4$ until the solution just turned pink. Subsequently 2 ml of sample digest were drawn into a 10-ml disposable syringe, followed by the addition of 2 ml reductant, and partitioning. The mercury was partitioned between liquid and air on a vortex mixer by drawing the syringe back to 10 ml (leaving a 6-ml air space). The vapor was then injected into a specially constructed 3-ml (total volume) glass absorption cell which had been mounted on the burner assembly of a Perkin-Elmer 303 atomic absorption spectrophotometer. A Westinghouse hollow cathode mercury lamp was used as an energy source. Three sets of blanks and three sets of standards consisting of 10, 20, and 30 ng mercury ($HgCl_2$) in triplicate were interspersed within a given sample run.

Calibration

During the analyses, aliquots of National Bureau of Standards Orchard Leaves No. 1571 were routinely analyzed for each element (Table 2). Similar standardizations conducted by Knauer (1972) during his study of metals in the northern anchovy, *Engraulis mordax*, and an interlaboratory calibration using both the destructive analytical techniques with atomic absorption spectrophotometry and non-destructive activation analysis (Knauer 1972; Goldberg 1972), indicate that our standardizations compare well with other laboratory analyses for these elements (Table 2).

[3]Reference to trade names does not imply endorsement by the National Fisheries Service, NOAA.

TABLE 2.—Comparative standardizations of elemental concentrations in National Bureau of Standards Orchard Leaves No. 1571 in micrograms per gram (Hg in nanograms per gram).

Laboratory	Hg $\bar{x}$	Hg c.v.	Cu $\bar{x}$	Cu c.v.	Ni $\bar{x}$	Ni c.v.	Ag $\bar{x}$	Ag c.v.	Cd $\bar{x}$	Cd c.v.	Pb $\bar{x}$	Pb c.v.
National Bureau of Standards	155	± 15	12.0	± 0.3	1.3	± 0.2			0.11	± 0.02	45.0	± 3.0
Hopkins Marine Station[1]												
Knauer	160	± 17	12.0	± 1.0	0.6	± 0.3	<0.05		0.21	± 0.1	41.0	± 3.8
Gilmartin and Revelante	166	± 22	10.0	± 1.0	2.3	± 0.4	0.15	± 0.04	0.30	± 0.1	41.0	± 4.3
Skidaway[1]	150	± 30	9.9	± 0.5					0.32	± 0.06	40.9	± 3.3
Battelle-Northwest[2]	180	± 20	11.2	± 1.3			<0.02		0.23	± 0.06		
Puerto Rico Nuclear Center[2]	170	± 50	11.8								[1]50.0	

[1]Flameless atomic absorption spectroscopy.
[2]Neutron activation analysis.

RESULTS

The six metals studied are considered from the viewpoint of differences in concentrations between the two species, variable concentrations in different tissues, and seasonal variations. Results are expressed in $\mu g\ g^{-1}$ wet weight for all elements except mercury, which is expressed in $ng\ g^{-1}$ wet weight. These can be converted to dry weight using the factors presented in Table 3.

Mercury

The seasonal distribution of mercury in various tissues in both the sardine and anchovy ranged from 5 to 610 $ng\ g^{-1}$ wet weight (Table 4). During

TABLE 3.—Sample size, length data, and wet:dry ratio for sardine and anchovy tissues analyzed for metal concentrations.

Date	n	Length (cm) Mean	Range	Wet:dry weight ratios Skin	Gills	Muscle	Digest.	Liver	Kidney	Gonad	Brain
Sardine:											
9 June 72	6			2.18	3.81	3.79	3.90	2.80			
10 July 72	6	12.90	12.7-13.2	1.38	4.57	3.71	3.22	3.56			
17 Aug. 72	6	16.14	15.5-16.5	2.36	4.62	4.04	4.48	3.47			
29 Sept. 72	5	15.28	14.6-16.0	1.53	4.30	3.54	2.43	3.76			
31 Oct. 72	6	17.85	7.0-18.8	1.56	4.36	3.55	2.33	4.64			
5 Dec. 72	6	15.08	14.4-16.0	1.82	4.14	3.86	4.00	1.67			
28 Mar. 73	6	17.69	16.7-18.3	1.88	5.31	3.94	4.45	4.04			
4 May 73	16	15.29	14.7-16.0	1.87	4.34	3.90	4.49	3.58	3.20	3.78	
8 May 73	51	15.39	14.1-17.4	1.81	4.44	4.10	4.58	3.47	2.87	3.99	3.94
24 May 73	49	14.93	14.1-15.8	2.05	4.09	3.88	4.40	3.41	3.78	4.69	4.23
6 June 73	45	15.54	14.6-16.6	2.23	4.17	3.70	3.54	3.55	3.51	3.69	4.04
Mean				1.88	4.38	3.82	3.80	3.45	3.34	4.04	4.07
Anchovy:											
9 June 72	6			1.73	3.92	3.47	2.65	2.56			
10 July 72	6	12.67	12.4-13.0	1.68	4.96	3.74	2.22				
17 Aug. 72	6	14.50	13.6-15.8	1.34	4.12	3.12	1.96	2.81			
3 Oct. 72	6	13.98	13.3-14.8	1.30	4.75	3.23	2.06	3.32			
31 Oct. 72	6	14.52	14.2-14.8	1.50	4.86	2.97	2.58	3.99			
6 Dec. 72	6	14.43	14.2-14.6	1.36	5.64	3.49	3.33	3.70		4.72	
29 Mar. 73	6	14.40	14.1-14.6	1.87	6.92	4.53	3.41	3.84			
24 May 73	60	13.37	12.2-14.8	1.81	3.70	3.89	4.16	3.35	3.19	4.09	3.81
6 June 73	52	14.75	13.2-16.6	2.52	4.10	4.03	5.21	3.46	4.32	3.56	4.06
Mean				1.68	4.77	3.61	3.06	3.38	3.76	4.12	3.94

TABLE 4.—Concentrations of total mercury ($ng\ g^{-1}$ wet weight) in tissues of sardine *Sardina pilchardus* and anchovy *Engraulis encrasicholus* from the Adriatic Sea.

Date	Skin[1]	Gills	Muscle	Digest.[1]	Liver	Kidney	Gonads	Brain	Tot. fish
Sardine:									
9 June 72	70		105	ND					80
10 July 72	35		40	ND					30
17 Aug. 72	10		135	90					110
29 Sept. 72	25		95	60					75
31 Oct. 72	35		115	110					105
5 Dec. 72	5		85	80					65
28 Mar. 73	105	25	115	100	155				100
4 May 73	30	35	80	80	160	260	20	15	60
8 May 73	60	35	90	115	215	455	40	35	85
24 May 73	45	30	95	60	210	220	30	35	80
6 June 73	70	45	120	115	210	330	75	35	165
Mean	45	35	100	75	190	315	40	30	85
Anchovy:									
9 June 72	75		120	ND					105
10 July 72	40		75	125					75
17 Aug. 72	55		215	ND					190
3 Oct. 72	ND		165	ND					140
31 Oct. 72	200		155	ND					160
6 Dec. 72	190		215	185					165
29 Mar. 73	70	25	85	140	215	295			65
24 May 73	80	45	70	110	255	370	35	25	75
6 June 73	145	60	175	215	415	610	80	35	170
Mean	95	45	140	85	295	425	60	30	125

[1]ND = not detected.

the early part of the study period, insufficient material was available to determine levels in certain tissues, but very significant species differences were noted between fish collected at the same point in time. In most instances mercury was present in greater amounts in specific anchovy tissues and the mean whole fish concentration was about 50% higher in anchovies.

The highest concentrations of mercury were noted in the liver and kidneys. On an annual mean basis the skin and gills of the sardine contained relatively low levels of mercury relative to other body tissues. In contrast, anchovy skin contained higher levels, especially during winter months when concentrations of 190-200 ng g^{-1} wet weight were observed. The greatest seasonal variation occurred in the digestive tract, where mercury ranged from not detected to 215 ng g^{-1}.

Copper

Copper levels ranged from 0.6 to 8.5 $\mu g\ g^{-1}$ wet weight (Table 5). As with mercury, anchovy tissues often contained higher concentrations of copper than corresponding sardine tissues, although the differences between the two species were not nearly so pronounced. The highest concentrations were observed in the liver of both species, with the skin of the anchovy consistently having significantly higher concentrations of copper than that of the sardine. On occasion the digestive tract of the anchovy contained up to 5.4× the concentrations in comparable sardine samples.

TABLE 5.—Concentrations of copper ($\mu g\ g^{-1}$ wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin	Gills	Muscle	Digest.	Liver	Total fish
Sardine:						
9 June 72	1.8	1.0	0.9	1.4	3.7	1.09
10 July 72	1.5	0.9	1.2	1.5	—	1.05
17 Aug. 72	1.2	0.6	0.9	1.0	2.5	0.96
29 Sept. 72	1.2	0.7	1.1	0.8	3.4	0.94
31 Oct. 72	0.9	0.7	0.9	1.4	2.1	0.97
5 Dec. 72	1.9	1.1	1.0	1.7	3.5	0.98
Mean	1.4	0.8	1.0	1.3	3.0	1.0
Anchovy:						
9 June 72	1.8	0.8	0.7	1.7	4.0	1.05
10 July 72	2.0	0.9	0.6	1.9	2.8	0.96
17 Aug. 72	3.1	0.8	0.8	2.9	3.9	1.09
3 Oct. 72	[1]17.5	0.8	0.8	4.3	3.2	1.52
31 Oct. 72	2.8	0.8	0.8	3.3	1.0	1.14
6 Dec. 72	2.5	0.6	0.6	1.5	8.5	0.98
Mean	2.4	0.8	0.7	2.6	3.9	1.1

[1]Suspect value — excluded from mean.

Nickel and Silver

In contrast with mercury and copper, the concentrations of nickel and silver rarely showed significant differences between the two species. Nickel was consistently detected in muscle tissue whereas silver was not, and nickel was occasionally observed in anchovy livers but not sardine (Tables 6, 7). Although data indicate higher concentrations in the gills and skin, these may be artifacts introduced by scatter caused by bone matrix in the gills and clays in the skin. The concentrations reported are therefore considered maximal estimates.

TABLE 6.—Concentrations of nickel[1] (μg^{-1} wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin	Gills	Muscle[2]	Digest.	Liver[2]	Total fish
Sardine:						
9 June 72	1.3	0.9	ND	0.3	ND	0.54
10 July 72	2.7	0.8	0.5	0.3	ND	0.53
17 Aug. 72	2.2	0.5	ND	0.1	ND	0.56
29 Sept. 72	2.9	0.5	0.3	1.0	ND	0.56
31 Oct. 72	1.5	0.7	0.3	ND	ND	0.59
5 Dec. 72	4.5	1.0	ND	0.6	ND	0.59
Mean	2.5	0.7	0.2	0.4	ND	0.6
Anchovy:						
9 June 72	1.7	0.9	0.3	0.4	ND	0.56
10 July 72	1.7	0.6	0.4	1.7	0.3	0.74
17 Aug. 72	1.1	0.2	0.3	0.6	0.2	0.58
3 Oct. 72	1.4	0.8	0.3	0.3	ND	0.46
31 Oct. 72	3.4	0.7	0.2	0.6	1.1	0.64
6 Dec. 72	5.8	0.9	0.2	0.9	ND	0.85
Mean	2.5	0.7	0.3	0.8	0.3	0.6

[1] = maximal estimates due to matrix problem.
[2]ND = not detected.

TABLE 7.—Concentrations of silver[1] ($\mu g\ g^{-1}$ wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin[2]	Gills	Muscle[2]	Digest.[2]	Liver[2]	Total fish
Sardine:						
9 June 72	0.3	0.1	ND	ND	ND	<0.09
10 July 72	0.3	0.1	ND	ND	ND	<0.08
17 Aug. 72	0.4	0.2	ND	ND	ND	<0.10
29 Sept. 72	0.6	0.1	ND	ND	ND	<0.10
31 Oct. 72	0.2	0.2	ND	ND	ND	<0.09
5 Dec. 72	0.7	0.2	ND	<0.1	ND	0.10
Mean	0.4	0.2	ND	ND	ND	0.1
Anchovy:						
9 June 72	0.4	0.1	ND	ND	ND	<0.08
10 July 72	0.5	0.1	ND	ND	ND	<0.08
17 Aug. 72	0.4	0.2	ND	ND	ND	0.08
3 Oct. 72	0.2	0.2	ND	ND	ND	0.09
31 Oct. 72	ND	0.2	ND	ND	ND	<0.07
6 Dec. 72	0.5	0.1	ND	<0.1	ND	<0.10
Mean	0.3	0.2	ND	ND	ND	0.1

[1] = maximal estimates due to matrix problem.
[2]ND = not detected.

Cadmium

Concentrations of cadmium in various anchovy and sardine tissues ranged from less than 0.1 to 1.4 $\mu g\ g^{-1}$ wet weight (Table 8). No significant difference was observed between the two species, except for the anchovy liver which had consistently higher levels than all other tissues. Higher concentrations occurred in the skin of both species.

Lead

Lead concentrations in sardine tissues paralleled those in the anchovy (Table 9). High concentrations occurred in the gills and skin of both species, and a tendency for higher levels in anchovy liver late in the year was observed. The lowest values tended to occur in muscle tissue, with seasonal means ranging from not detected to 1.2 $\mu g\ g^{-1}$ wet weight.

TABLE 8.—Concentrations of cadmium ($\mu g\ g^{-1}$ wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin	Gills	Muscle[1]	Digest.[1]	Liver[1]	Total fish
Sardine:						
9 June 72	0.2	0.2	<0.1	0.1	0.2	0.11
10 July 72	0.3	0.2	<0.1	0.3	ND	0.11
17 Aug. 72	0.4	0.1	ND	ND	0.4	0.10
29 Sept. 72	0.5	0.1	ND	ND	0.2	0.09
31 Oct. 72	0.3	0.1	ND	0.1	0.1	0.10
5 Dec. 72	0.5	0.2	ND	0.3	0.1	0.11
Mean	0.4	0.2	<0.1	0.1	0.2	0.1
Anchovy:						
9 June 72	0.4	0.2	<0.1	0.2	0.9	0.16
10 July 72	0.3	0.3	0.1	0.4	0.5	0.13
17 Aug. 72	0.5	0.3	<0.1	0.2	0.7	0.13
3 Oct. 72	0.2	0.1	ND	0.2	0.5	0.09
31 Oct. 72	0.4	0.2	<0.1	0.2	ND	0.12
6 Dec. 72	0.6	0.1	<0.1	0.2	1.4	0.20
Mean	0.4	0.2	<0.1	0.2	0.7	0.1

[1]ND = not detected.

TABLE 9.—Concentrations of lead ($\mu g\ g^{-1}$ wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin	Gills	Muscle[1]	Digest.[1]	Liver[1]	Total fish
Sardine:						
9 June 72	4.5	3.0	0.4	ND	ND	1.23
10 July 72	4.9	4.5	0.1	ND	ND	0.94
17 Aug. 72	4.3	2.6	ND	ND	ND	0.82
29 Sept. 72	5.3	1.9	ND	2.2	ND	0.84
31 Oct. 72	3.3	2.4	ND	0.7	ND	1.38
5 Dec. 72	6.8	3.1	ND	0.3	ND	1.40
Mean	4.9	2.9	0.1	0.5	ND	1.1
Anchovy:						
9 June 72	2.7	4.3	ND	ND	ND	0.99
10 July 72	5.2	3.7	ND	0.4	ND	0.99
17 Aug. 72	5.7	3.9	ND	0.3	1.1	0.51
3 Oct. 72	1.6	2.6	ND	1.3	1.5	0.73
31 Oct. 72	7.0	3.1	1.2	0.7	3.4	1.16
6 Dec. 72	6.5	3.9	0.3	0.4	[2]11.0	1.37
Mean	4.8	3.6	0.3	0.5	1.2	1.0

[1]ND = not detected.
[2]Suspect value — excluded from mean.

DISCUSSION

The six heavy metals considered during this study fall into two groups with regard to distribution in tissues and differences in concentrations between the two species: nickel, silver, cadmium, and lead, with no major interspecific differences and the highest concentrations occurring in the skin and gills, and mercury and copper, with marked interspecific differences and the highest concentrations occurring in internal tissues.

The highest concentrations of nickel, silver, cadmium, and lead were observed in the skin and gills, perhaps associated with adsorption. A significant interspecific difference was observed with nickel and lead, with these elements being nondetectable in the sardine liver but frequently being detected in anchovy liver, suggesting a difference in feeding habits and/or migration routes of the two species.

A tendency for increasing lead concentrations in the skin during winter was evident, related perhaps to wind-induced roiling of sediments into the water column during this period. The northern Adriatic is known to have relatively high concentrations of metal pollutants in the bottom sediments (Selli et al. 1972; Štirn pers. commun. 1973). A comparison of the concentrations of these metals in various tissues of the Adriatic and northern anchovies (Table 10) indicated that both nickel and cadmium occurred at approximately the same level. The relatively high nickel concentrations reported for the skin of the Adriatic anchovy could be an artifact introduced by analytical techniques (Table 2).

Copper and mercury showed a very different distribution pattern, with concentrations highest in the digestive tract and liver of the two clupeids, and seasonal means 2 to 3× greater than in the skin and gills, suggesting that ingestion may be the primary entry route into the organism. Concentrations in anchovy muscle tissue were markedly higher than in the sardine, contrasting with Establier's (1972) report that there were no differences in mercury concentration between these species off northwest Africa.

TABLE 10.—Mean elemental concentrations in *Engraulis mordax* collected from Monterey Bay, Calif. (Pacific) from Knauer (1972) and in *E. encrasicholus* from Rovinj, Yugoslavia (Adriatic) (mercury: ng g^{-1} wet weight: other elements: $\mu g\ g^{-1}$ wet weight).

Element	Location	Skin	Gills	Muscle	Digest.	Liver	Gonads
Mercury	Pacific	10	30	40		90	15
	Adriatic	95	45	140		295	55
Copper	Pacific	1.6	3	1.6	5	3	2
	Adriatic	2.4	0.8	0.7	2.6	3.9	
Nickel	Pacific	0.4	0.7	ND	1.1	ND	ND
	Adriatic	2.5	0.7	0.3	0.8	0.3	
Silver	Pacific	0.2	0.4	0.01	0.07	ND	0.4
	Adriatic	0.3	0.2	ND	ND	ND	
Cadmium	Pacific	0.2	0.3	0.03	2.8	1	0.3
	Adriatic	0.4	0.2	<0.1	0.2	0.7	
Lead	Pacific	3	4.8	0.2	1.2	ND	0.2
	Adriatic	4.8	3.6	0.3	0.5	1.2	

ND = not detected.

The calculated concentrations of mercury in the whole sardine range from 100 to 645 ng g^{-1} dry weight, with a seasonal mean of 320. These values compare favorably with the 580 ng g^{-1} dry weight reported by Ui (1971) for sardine collected in coastal waters 2 to 3 km north of Porto Corsini, on the Italian side of the northern Adriatic. Levels of mercury found in the northern Adriatic anchovy were relatively high when compared with levels in the same or similar species in other parts of the world. Mean concentrations of 140 ng g^{-1} wet weight were found in muscle tissue, and values in excess of 200 ng g^{-1} were observed (Table 4). The same species from the Gulf of Cádiz and off northwestern Africa contained 60 and 50 ng g^{-1} wet weight respectively (Establier 1972); and the northern anchovy, *Engraulis mordax*, occupying the same ecological niche (see Baxter 1967), contained concentrations in muscle tissue averaging 40 ng g^{-1} wet weight (Knauer and Martin 1972). These last data are directly comparable, since the analyses were conducted in the same laboratory using the same techniques and equipment.

Short-lived, low trophic level fish such as the anchovy have a tendency to concentrate low levels of mercury relative to longer-lived higher order carnivores, e.g. tunas and billfishes (Rivers et al. 1972), yet the higher concentrations of mercury in internal tissues indicate an accumulation in the Adriatic anchovy as well. However, it should be noted that the source of such mercury is not necessarily lower trophic level organisms. On entering the sea, mercury is immediately bound to proteinaceous materials, and if not adsorbed or absorbed by organisms, is often present in detritus/matrixlike suspended matter (see Keckes and Miettinen 1972, for review). Since massive amounts of suspended matter are found in feeding areas, filter feeders cannot avoid ingesting it (Leong and O'Connell 1969).

While mercury input to the sea results from a combination of natural processes, such as weathering and atmospheric fallout, and from various anthropogenic processes, a number of recent studies have focused on the pollution resulting from increasing urbanization and industrialization along the northern Adriatic coast, in particular within the Po River watershed (Štirn 1965, 1970; Majori, Morelli, Diana, and Rausa 1967; Majori, Rausa, Morelli, and Diana 1967; Majori et al. 1968; Majori 1968; Panella 1968a, b, 1970; Cescon and Grancini 1971; General Fisheries Council for the Mediterranean 1972). Three factories in northern Italy use the same acetaldehyde process as the Japanese Minimata plant (Ui and Kitamura 1971), and two of these are located on the coast at Ravenna and Venice, offshore of which are the spring spawning grounds of the anchovy (Štirn 1969). In addition, the wintering grounds of the anchovy lie to the south, in an area influenced by the Po River (Štirn 1969; Piccinetti 1970).

The rate of mercury elimination by fish is slow, e.g. 267-700 days (Keckes and Miettinen 1972). This time scale easily spans annual migrations encompassing the northern Adriatic and emphasizes the necessity for international consideration of the potential pollution of the region. Although the levels of mercury observed in this study are well within the tolerances established by most countries (e.g. 200 ng g^{-1} muscle wet weight in Switzerland, 500 ng g^{-1} in the United States, and 1,000 ng g^{-1} in Italy and Japan), it is likely that with increasing anthropogenic input to the northern Adriatic, concentrations will increase, perhaps to prohibitory levels. Thus it is essential that monitoring continue, especially of the clupeid *Engraulis encrasicholus*, which not only concentrates mercury to a greater degree than the sardine, but which may represent one of the few significantly underutilized fish resources of the northern Adriatic Sea.

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THE CORRELATION BETWEEN NUMBERS OF VERTEBRAE AND LATERAL-LINE SCALES IN WESTERN ATLANTIC LIZARDFISHES (SYNODONTIDAE)[1]

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ABSTRACT

The 10 species of Synodontidae in the western Atlantic have a positive correlation between numbers of vertebrae and pored lateral-line scales. A ratio of close to 1:1 exists for all species, with individuals having from four more to two fewer scales than vertebrae, and the majority having at least one more scale than vertebrae. Geographic variation is suggested by vertebral counts of four species, and possible taxonomic heterogeneity is indicated by the counts of a fifth species. Scale counts are bilaterally symmetrical in most individuals and differ by one scale in most of the rest. Vertebral and scale counts are given for type specimens at the U.S. National Museum of Natural History.

The principal purpose of this paper is to describe the complements and correlations of vertebrae and pored lateral-line scales in samples of the western Atlantic species of Synodontidae, as a contribution to the knowledge of their morphology and to facilitate specific identification of various life history stages.

The species of the lizardfish family Synodontidae have been distinguished in part by differences in number of pored lateral-line scales for juvenile and adult stages (e.g. Norman 1935; Anderson et al. 1966a, b) and in number of myomeres for larval and prejuvenile stages (Gibbs 1959). Accurate scale counts may be impossible in damaged or small specimens, and myomeres are difficult to count in all but young stages. Numbers of myomeres in individual fish are equal or about equal to numbers of vertebrae, but species complements of vertebrae in synodontids have not been analyzed or utilized.

For the 10 species of lizardfishes in the western Atlantic, we have determined that:

1) complements of vertebrae and intraspecifically variable with a relatively normal distribution around the mean (as occurs with complements of scales and myomeres);
2) numbers of vertebrae have a positive correlation to numbers of pored lateral-line scales;
3) in individuals, the number of vertebrae is in a ratio of close to 1:1 to the number of pored lateral-line scales, with scales ranging from two less to four more than vertebrae in our samples, and the majority of specimens of all species having more scales than vertebrae.

MATERIALS AND METHODS

Specimens used in this study are in the collections of the Florida State Museum (formerly in the Tropical Atlantic Biological Laboratory, Miami, Fla. and the Biological Laboratory at Brunswick, Ga.), the Academy of Natural Sciences of Philadelphia, and the U.S. National Museum of Natural History (USNM). Some of the specimens used in these analyses were specifically selected from material previously reported by us (Anderson et al. 1966a) to encompass high and low values in scale counts of the various species or to obtain geographic coverage.

Identifications, measurements, and counts were made as described by Anderson et al. (1966a) with the following additions:

Vertebrae—counted from the anteriormost centrum articulating with the occipitals to and

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including the triangular-shaped last or ultimate centrum articulating with the hypural bones. All counts were made from X rays. Vertebral counts for individual specimens are used twice in correlations with paired (bilateral) scale counts. Specimens with obvious abnormalities in vertebral structure were not included in the tabulations.

Pored lateral-line scales—counted from the first pored scale in the lateral line to and including the last pored scale in the lateral line, lateral to the median base of the caudal-fin rays. Specimens with one or more scales missing from the lateral line were included in the tabulations, if the position of the scale pockets or the remaining scales were adequate to allow an accurate reconstruction. Bilateral counts were made for each specimen, and the counts for both sides of each fish were included in all tables and in the correlations with vertebrae. The term scale or scales refers specifically to pored scales in the lateral line.

RESULTS

Vertebrae

Vertebrae in our samples of the 10 western Atlantic species range from 44 to 62. We know of one higher count for a synodontid—the holotype of *Synodus ulae* from Hawaii has 64 vertebrae. Statistics based on vertebral samples for the western Atlantic species are listed in Table 1 and graphically depicted in Figure 1. Samples of at least six of the species are probably too small (and possibly too heterogeneous) to adequately define the ranges of vertebral complements for these species. This is obvious from comparison of skewedness of the range and/or standard deviations and the relatively large values of the standard errors. For the two species for which we have the largest and most reliable samples, *Sy. foetens* and *Sy. intermedius*, the relation of variance to meristic complement is similar to that we have noted in some other fish families—the species with the larger number or larger range of elements has the greater variance. The extremely high variance and extensive range of vertebrae in *Saurida caribbaea* suggest a taxonomic or ontogenetic problem as yet unidentified.

Intraspecific geographic variation in these lizardfishes has not been investigated, but our limited samples of four of the species suggest that it may exist. *Synodus intermedius* appears to have fewer vertebrae in tropical continental waters and more in insular areas than in temperate and subtropical continental waters.

Area	n	$\bar{x}$
U.S.—Mexico	37	48.2
Honduras—Surinam	21	47.6
Brazil	25	48.6

These samples are relatively homogeneous, and the means of the three samples are significantly different ($P < 0.01$, anova). *Synodus foetens* may have a parabolic cline in mean vertebral number, with lower average numbers in tropical areas and higher average numbers to the more temperate north and south.

Area	n	$\bar{x}$
U.S.—Mexico	98	59.6
Honduras—Surinam	9	58.1
Brazil	10	59.6

TABLE 1.—Statistics from numbers of vertebrae, numbers of pored lateral-line scales, and correlation coefficients of the two variates from samples of the 10 species of western Atlantic Synodontidae.

Species	Vertebrae						Scales				Correlation (r)
	No.	Range	Mean	SD	SE	Var.	No.	Range	Mean	Var.	
Synodus foetens	118	56-62	59.4	1.4082	0.1296	1.98	236	57-63	61.1	2.11	0.86
Synodus saurus	14	56-58	57.6	0.6667	0.1693	0.40	28	58-60	58.9	0.57	0.20
Synodus synodus	11	55-57	55.7	0.9045	0.2727	0.82	20	55-58	58.1	0.68	0.44
Synodus intermedius	85	47-50	48.2	0.7661	0.0831	0.59	170	47-51	49.1	0.94	0.76
Synodus poeyi	19	44-48	45.6	1.2996	0.2965	1.69	38	43-48	45.8	3.00	0.83
Trachinocephalus myops	11	54-57	55.4	0.9244	0.2787	0.85	22	54-58	56.4	0.92	0.37
Saurida brasiliensis	10	46-48	46.7	0.8233	0.2603	0.68	20	47-49	48.2	0.56	0.52
Saurida normani	11	49-52	50.9	1.1362	0.3423	1.30	22	52-56	54.0	1.38	0.84
Saurida suspicio	11	49-52	51.3	0.9045	0.2727	0.82	22	52-54	52.8	0.47	0.50
Saurida caribbaea	27	48-58	54.2	2.6651	0.5129	7.10	38	51-60	56.2	8.69	0.96

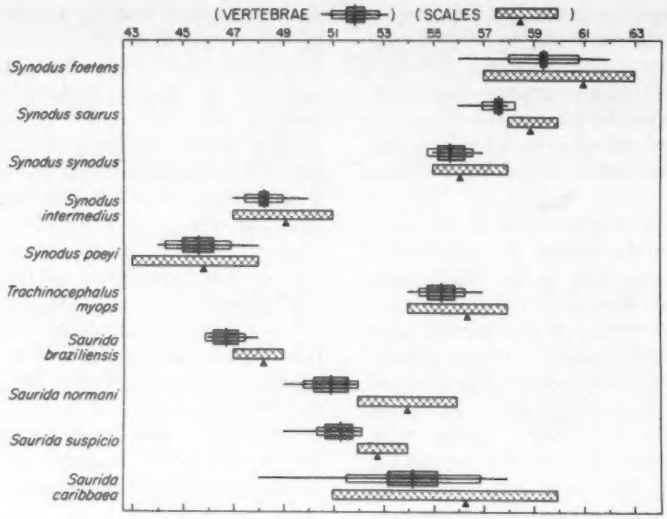

FIGURE 1.—Numbers and statistics of vertebrae and scales of the 10 species of western Atlantic Synodontidae. Vertebrae: range—horizontal line; mean—vertical line; standard deviation, one on each side of the mean—open rectangle; standard error—two on each side of the mean—shaded rectangle. Scales: range—cross-hatched bar; mean—small triangle.

Synodus saurus from the eastern Atlantic (5 specimens) had a range in vertebrae of 55-59, greater than the western Atlantic (14 specimens) vertebrae range of 56-58. *Trachinocephalus myops* had varying but similar vertebral ranges in small samples encompassing its extensive geographic range.

Area	n	$\bar{x}$	*Range*
U.S.—Brazil	11	55.4	54-57
Nigeria	1	55.0	55
Philippines	7	53.1	52-54
Hawaii	5	54.8	54-55

Abnormalities in vertebral structure (specimens not included in the tables or figure) occurred in 11 of 317 western Atlantic specimens examined. In six, pairs of vertebrae were shortened with irregular and expanded ossifications at their adjoining ends. In five, a single centrum in the caudal region was elongated and had two neural spines (in two), two hemal spines (in two), or double neural and hemal spines (in one).

Scales

Pored lateral-line scales in our samples of the 10 western Atlantic species range from 43 to 63 (Table 1). We have not confirmed any higher or lower values for these or other species of the family. Ranges in scale complements that we have confirmed for specimens from the western Atlantic, with clarification where these ranges differ from those given by Anderson et al. (1966a), are:

Synodus foetens 57-64; the range of 56-65 given by Anderson et al. was in error, as determined by our reexamination of the material originally reported. *Synodus saurus* 56-60; the range of 55-62 given by Anderson et al. included a low count for an eastern Atlantic specimen and a published but unsubstantiated high count. *Synodus synodus* 54-59. *Synodus intermedius* 47-51; the range of 45-52 given by Anderson et al. was in error, as determined by our reexamination of the material originally reported. *Synodus poeyi* 43-48. *Trachinocephalus myops* 53-59; the

range of 51-61 reported by Anderson et al. was based on previously published records from other geographic areas. *Saurida brasiliensis* 43-49; the range of 40-50 reported in Anderson et al. was based on a low count previously published and currently unconfirmable and on a high count that we have since confirmed in a specimen from the eastern Atlantic. *Saurida normani* 51-56. *Saurida suspicio* 52-54; a high count of 56 previously published has not been confirmed by us. *Saurida caribbaea* 51-60; examination of additional specimens has enlarged the range of 54-60 given by Anderson et al.

Many of the specimens used in the confirmations above are not included in Table 1, because corresponding vertebral counts were not made.

Bilateral symmetry in scale numbers characterized one-half to three-quarters of the specimens of each species. In the total sample, 62% were bilaterally symmetrical. Asymmetry appears to be random, 20% having more scales on the left side and 18% having more scales on the right side. Asymmetry was of only one scale difference in all species, except in our largest species sample. In *Sy. foetens*, which also has the greatest number of scales, of 118 specimens 3 had two more scales on one side than the other, 52 had one more scale on one side than the other, and 63 were bilaterally symmetrical.

Correlations

Frequency distributions of numbers of vertebrae and associated numbers of pored lateral-line scales are shown for the two species for which we examined the largest number of specimens, *Sy. foetens* (Table 2) and *Sy. intermedius* (Table 3). The trend of positive correlation is apparent from visual inspection of both tables. The coefficients of correlation (Table 1) document the positive nature of the correlation, *Sy. foetens* (r = 0.86) and *Sy. intermedius* (r = 0.76) (Table 1).

The same kinds of data for the other eight species are given below, with number of vertebrae separated by a hyphen from the number of scales and followed in parentheses by the frequency for that combination:

Synodus saurus, vertebrae 56-58 scales (2), 57-58(1), 57-59(4), 57-60(1), 58-58(7), 58-59(8), 58-60(5). *Synodus synodus*, 55-55(3), 55-56(7), 56-55(1), 56-56(1), 56-57(2), 57-55(1), 57-56(2), 57-57(2), 57-58(1). *Synodus poeyi*, 44-43(4), 44-44(2), 44-45(3), 44-46(1), 45-43(1), 45-44(2), 45-45(1), 45-46(2), 46-44(1), 46-45(2), 46-46(2), 46-47(9), 47-48(4), 48-48(4). *Trachinocephalus myops*, 54-56(3), 54-57(1), 55-54(1), 55-55(2), 55-56(3), 55-57(2), 56-56(1), 56-57(5), 56-58(2), 57-56(1), 57-57(1). *Saurida brasiliensis*, 46-47(4), 46-48(6), 47-49(6), 48-48(3), 48-49(1). *Saurida normani*, 49-52(3), 49-53(1), 50-53(2), 51-53(1), 51-54(3), 51-55(4), 52-54(2), 52-55(5), 52-56(1). *Saurida suspicio*, 49-52(1), 49-53(1), 51-52(7), 51-53(3), 52-53(7), 52-54(3). *Saurida caribbaea*, 48-51(2), 49-51(3), 50-52(2), 52-53(3), 52-54(1), 54-55(1), 54-56(1), 54-58(2), 55-57(2), 55-58(3), 55-59(5), 56-57(3), 56-58(4), 56-59(1), 57-59(2), 58-60(2).

TABLE 2.—Frequency distributions of numbers of vertebrae and pored lateral-line scales in 118 *Synodus foetens*.

Scales	Vertebrae						
	56	57	58	59	60	61	62
63	—	—	—	—	10	25	2
62	—	—	—	4	57	15	2
61	—	—	4	15	21	4	—
60	—	1	19	14	2	—	—
59	4	15	5	2	2	—	—
58	4	7	—	1	—	—	—
57	—	1	—	—	—	—	—

TABLE 3.—Frequency distributions of numbers of vertebrae and pored lateral-line scales in 85 *Synodus intermedius*.

Scales	Vertebrae			
	47	48	49	50
51	—	1	9	2
50	—	5	37	2
49	2	44	16	—
48	26	21	—	—
47	2	3	—	—

The correlation coefficients of the samples for all species are positive, ranging from 0.96 for *Sa. caribbaea* to 0.20 for *Sy. saurus* (Table 1). The species with the larger number of specimens (19 to 118) generally had the higher correlation coefficients (r 0.76 to 0.96). Of the species with a lesser number of specimens (11 to 14), one had a high positive value (0.84), and the others were low (0.20 to 0.52). We suspect that the relatively low value of positive correlation for five of the species is due to the small and somewhat heterogeneous samples used for these species.

Statistics describing the samples of vertebrae and scales for each species (from Table 1) are illustrated in Figure 1. The nature of positive

correlation of vertebrae and scales for the 10 species is apparent in this figure.

The ratio of scales to vertebrae is nearly 1:1 for the 10 species, but in each species the total number of scales averages slightly more than the total number of vertebrae (50% or more of the scale counts in any species are greater than the vertebral counts). In species of *Saurida* the number of scales averages from one to three more than the number of vertebrae and ranges from an equal number of each to four more scales than vertebrae. In species of *Synodus* and in *Trachinocephalus* the number of scales averages one or two more than the number of vertebrae and ranges from two fewer to three more scales than vertebrae. Of 118 *Sy. foetens* 10% had three more scales than vertebrae, 57% had two more scales, 27% had one more, 5% had an equal number, and 1% had one less scale than vertebrae.

The positional relationship of scales to vertebrae in lateral aspect was investigated. In a *Sy. foetens* with 62 pored lateral-line scales on each side and 60 vertebrae, pins were inserted at the posterior margins of certain numbered lateral-line scales on the left side, and the specimen was X-rayed. The first scale was lateral to the junction of the 4th and 5th centra, the 30th scale was lateral to the junction of the 32nd and 33rd centra, the 60th scale was lateral to the last centrum, and the last scale was lateral to the posterior ends of the hypural bones and overlapping anterior ends of the median caudal-fin rays. Similarly, in a *Sy. intermedius* with 49 scales on each side and 48 vertebrae the first scale was lateral to the 4th centrum, the 47th scale was lateral to the 48th centrum, and the last scale was lateral to the posterior ends of the hypural bones.

DATA ON TYPE SPECIMENS AT USNM

Counts of vertebrae and pored lateral-line scales on type specimens of 12 nominal species of Synodontidae in the U.S. National Museum of Natural History are recorded here for use in future studies. The four data items following the collection number for each type specimen are, in sequence, number of vertebrae, number of left-side scales, number of right-side scales, and standard length in millimeters:

Synodus binotatus Schultz, holotype USNM 140801, 53-54-ca. 54-86.5. *Synodus cinereus* Hildebrand, holotype USNM 53079, 57-58-59-112. *Synodus englemani* Schultz, holotype USNM 140815, 59-60-60-104. *Synodus evermanni* Jordan and Bollman, one of 11 syntypes USNM 41144, 47-48-48-142. *Synodus jenkinsi* Jordan and Bollman, holotype USNM 41171, 60-ca. 60-61-282. *Synodus lacertinus* Gilbert, holotype USNM 44300, 61-63-62-129. *Synodus marchenae* Hildebrand, holotype USNM 120171, 60-62-62-50.5. *Synodus sechurae* Hildebrand, holotype USNM 127829, 57-58-58-130. *Synodus simulans* Garman, paratype USNM 153607, 60-ca. 62-ca. 61-ca. 45. *Synodus ulae* Schultz, holotype USNM 52671, 64-ca. 63-ca. 63-177. *Saurida eso* Jordan and Herre, holotype USNM 57847, 59-62-61-290. *Saurida normani* Longley, holotype USNM 107330, 52-52-53-320.

In these type specimens the ratio of nearly 1:1 for number of vertebrae and scales suggests a positive correlation of these two variates in the species that they represent.

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ACUTE TOXICITY OF AMMONIA TO SEVERAL DEVELOPMENTAL STAGES OF RAINBOW TROUT, *SALMO GAIRDNERI*

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ABSTRACT

Median tolerance limits derived from 24-h bioassays demonstrated that fertilized eggs and alevins of rainbow trout, *Salmo gairdneri*, were not vulnerable to 3.58 ppm un-ionized ammonia at 10°C (pH 8.3). At the end of yolk absorption, rainbow trout fry increased in susceptibility dramatically; their median tolerance limit values were about 0.072 ppm, the same as for adult trout. Fertilization of eggs was not prevented in un-ionized ammonia solutions up to 1.79 ppm, the highest exposure tested.

Much information is available on the toxicity of ammonia to juvenile and adult trout, but the paucity of information on the toxicity of ammonia to fertilized eggs and larvae of teleosts is surprising since these life stages are often assumed to be relatively sensitive. Several studies have examined ammonia toxicity to adult trout (Lloyd 1961; Ball 1967; Wilson et al. 1969), including the effects of increased ammonia toxicity to trout at lower oxygen levels (Downing and Merkens 1955) and decreased toxicity at higher carbon dioxide levels (Lloyd and Herbert 1960). Temperature, oxygen, pH, carbon dioxide, and bicarbonate alkalinity influence the toxicity of ammonia and are discussed in a report by the European Inland Fisheries Advisory Commission (1970). Exposure of juvenile or adult salmonids to ammonia has been associated with decreased growth (Brockway 1950; Burrows 1964; Larmoyeux and Piper 1973), gill damage (Burrows 1964; Reichenbach-Klinke 1967), and other sublethal physiological effects (Reichenbach-Klinke 1967; Fromm and Gillette 1968; Lloyd and Orr 1969), and similar effects may occur with salmonid eggs and alevins. Exposure to ammonia has also been associated with increased incidence of disease in juvenile and adult salmonids (Burrows 1964; Larmoyeux and Piper 1973) and in salmonid alevins (Wolf 1957).

The only study of toxicity of ammonia to eggs and larvae (Penaz 1965) involved three stages of eggs and two stages of yolk fry of *Salmo trutta*. Penaz observed an increase in sensitivity of the eggs with age to brief (120 min) exposures to ammonia at pH 8 and temperatures of 5.68° to 3.56°C. A similar pattern was observed with longer exposures (10 h) of newly hatched and 12-day-old alevins to ammonia at pH 8 and temperatures of 11° and 16.9°C. The early eggs were resistant to the highest dose he tested—50 mg/liter of un-ionized ammonia. These data suggest changes in sensitivity with development, but the changes in lengths of exposure and temperature make it difficult to compare differences between eggs and alevins.

We used a series of bioassays to determine the stage of development at which eggs and larvae of rainbow trout, *Salmo gairdneri*, were most susceptible to acute ammonia toxicity. Such information is needed to establish realistic limits for survival of eggs and larvae in both natural and hatchery environments. Knowledge of concentrations of ammonia that may limit survival is particularly important in hatchery operations where it is advantageous to maintain the greatest density of fish and eggs per unit water flow.

MATERIALS AND METHODS

Freshly fertilized rainbow trout eggs were obtained from Bowden National Fish Hatchery, W.V., (courtesy of the U.S. Bureau of Sport Fisheries and Wildlife) and transported to the laboratory within 6 h.

About 2,000 of the eggs were poured under water into 4-inch-square trays with nylon screen bottoms at about 25 to 35 eggs per tray. For incubation the trays were put into a 10°C water

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bath that recycled through both charcoal and a gravel bacterial filter at a rate of 3 gallons/min. Ammonia levels were measured periodically and never attained 0.1 ppm. All ammonia analyses were made by separating ammonia by diffusion (Conway and Cooke 1939) and followed by nesslerization of the separated ammonia. For the ammonia bioassays, the small trays were transferred directly to the experimental medium. By conducting the bioassays in the same trays in which the eggs or larvae were incubated, we did not have to pipette them to other containers—a process that might have injured them.

Two series of duplicated ammonia toxicity bioassays were conducted according to standard procedures outlined by Doudoroff et al. (1951) and results were expressed as 24-h median tolerance limits (24-h TLm)[3]. The bioassays were conducted every 4 to 7 days from fertilization to the completion of yolk sac absorption. Toxicity of ammonia to adult rainbow trout (length 7-9 inches) was also measured with static bioassays (12 fish per concentration tested, 1 fish per 10-liter aquarium) at the same water temperature and pH used with the eggs and larvae.

All bioassays were conducted in aged tap water (total hardness 5.94 ppm as calcium carbonate at pH 7.8) adjusted to pH 8.3 with tris buffer (final concentration 0.05 M). Ammonia, in the form of ammonia sulfate, was added to arrive at the various test concentrations. The resulting conditions made the ammonia toxicity assays more severe than would normally be encountered because the toxicity of ammonia increases as pH increases due to the conversion of ionized NH_4^+ into the un-ionized NH_3 form. At 10°C and pH 8.3, 3.58% of the ammonia in water is un-ionized, considerably more than the 0.19% un-ionized ammonia at pH 7 (Trussell 1972).

Since the un-ionized form of ammonia has been identified as the toxic form, we report our results in units of un-ionized ammonia rather than total ammonia.

Several water quality parameters were measured at the beginning and end of the bioassays, since changes could affect the results. Ammonia levels never dropped below 93% of the initial bioassay concentrations during the course of the 24-h experiments. Very low levels of un-ionized ammonia (0.011 ppm) were detected in the control exposures after 24 h. The tris buffer prevented any changes in pH from occurring during the 24-h tests. Dissolved oxygen remained above 91% saturation in the shallow egg-alevein bioassay containers and above 88% saturation in the adult bioassays (measured with YSI oxygen probe).[4] Carbon dioxide was not measured in any of the bioassays.

We tested the influence of ammonia on egg fertilization and viability during the water-hardening stage by exposing some eggs to ammonia at Bowden Hatchery on the day our experimental eggs were collected. Approximately 200 to 300 eggs from one female were stripped into each of several pans containing tris buffered water (pH 8.3, temperature 8°-10°C), some with added ammonia at concentrations up to 1.79 mg/liter of un-ionized ammonia. Milt from at least two young males was stripped into each pan of water and eggs 15 to 30 s later. Buss and Corl (1966) determined that fertilization must be completed within the first 1 or 2 min because the sperm are viable in water for only a few seconds. By replacing the ammonia solutions with fresh water in one-half of the pans after 2 or 3 min of ammonia exposure and in the remaining pans after 1 h, we hoped to separate the effects of ammonia on fertilization per se from the effects on the viability of the fertilized eggs during the water-hardening stage of the first hour. The effects were measured by determining the percentage of eggs that hatched.

RESULTS AND DISCUSSION

Neither fertilized eggs, embryos, nor alevins (embryo after hatching) were susceptible to a 24-h exposure of un-ionized ammonia (3.58 mg/liter) until about the 50th day of development (Figure 1). At that time, susceptibility increased dramatically and continued to increase until most of the yolk was absorbed (when alevins became fry). The median tolerance limits (24-h TLm) for 85-day-old fry were 0.068 mg/liter, slightly less than the 0.097 mg/liter value we observed for adult trout; in the bioassays for both the fry and the adults, temperature was 10°C and pH was 8.3.

Buss and Corl (1966) found that the viability of eggs of brook trout, *Salvelinus fontinalis*, and

[3]24-h TLm = the concentration resulting in 50% survival after 24-h exposures.

[4]YSI = Yellow Springs Instrument Company, Inc., Yellow Springs, Ohio. Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

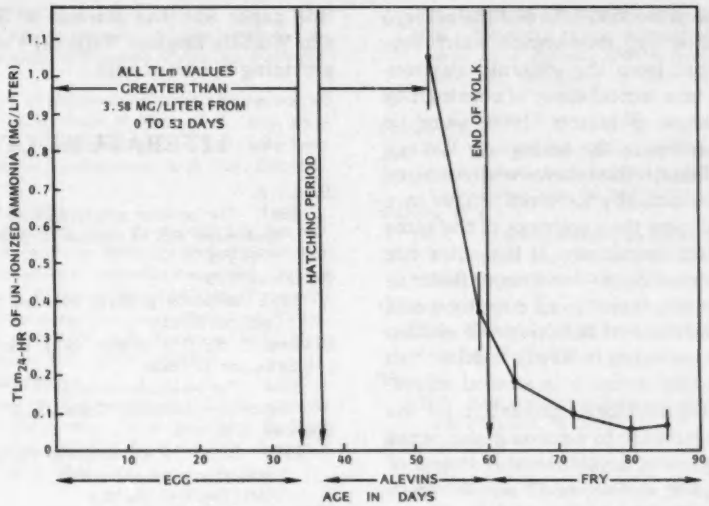

FIGURE 1.—Twenty-four-hour median tolerance limits (TLm) of un-ionized ammonia to eggs and alevins of rainbow trout (10°C, pH 8.3). Points indicate mean of two bioassays; bars indicate the range. Adult trout 24-h TLm was 0.097 mg/liter (10°C, pH 8.3).

brown trout, *Salmo trutta*, drops significantly after 15 s in water—in our experiments this was about the minimum time lapse between stripping eggs into the water and introduction of sperm. Because we did not control the time lapse before sperm introduction precisely enough, we cannot evaluate any subtle effects of ammonia on prevention of fertilization. It was obvious, however, that high ammonia concentrations did not cause complete loss of eggs or sperm (Table 1) because more than half of the eggs were fertilized at all ammonia exposures. No obvious differences in the percentages of eggs that hatched were noticed between ammonia exposures of 2 or 3 min and 1 h, even at the highest concentrations of un-ionized ammonia (1.79 mg/liter) we tested. The fertilization and water-hardening stages are similar to later stages (before 50 days of development) in their relative insensitivity to ammonia when compared with older fry with absorbed yolks (after about 60 days of development).

Our observations of great resistance of eggs and alevins of rainbow trout to ammonia toxicity are consistent with results of ammonia toxicity studies of Penaz (1965) and with other studies of other toxicants. Trout eggs and sac fry were only slightly susceptible to endrin at concentrations that seriously affected adults (Wenger 1973). Burdick et al. (1964) observed that a high proportion of lake trout, *Salvelinus namaycush*, fry from normal appearing eggs containing 2.95 ppm DDT or more died. The sensitive fry died at the completion of yolk absorption when feeding would normally begin. Eggs of "common trout" were less susceptible to anionic detergent toxicity (sodium alkylsulphate) than alevins, whose sensitivity continued to increase for 6 wk (Wurtz-Arlet 1959). Eggs of two salmonids were about one-tenth as sensitive to a commercial formulation of rotenone and derivatives as fry at the same temperature (Garrison 1968). A study of zinc toxicity by Skidmore (1965) showed that eggs of zebrafish, *Brachydanio rerio*, were relatively less susceptible than newly hatched fish.

It appears then that eggs and developing embryos are resistant to several toxicants, including ammonia. One obvious explanation for the resis-

TABLE 1. — Effect of ammonia on fertilization.

Concentration of un-ionized ammonia	Percentage[1] hatch at exposure of	
	2-3 min	1 h
0 mg/liter	66.8	68.4
0.0358 mg/liter	74.3	70.1
1.79 mg/liter	58.2	68.8

[1]Percentage hatch of each group of 250 eggs.

tance may be the protection afforded the embryo by the surrounding egg membranes which separate the internal from the external environment. However, in a second study of zinc toxicity to zebrafish embryos, Skidmore (1966) found no evidence of protection of the embryo by the egg membranes. He found that embryos with ruptured outer membranes actually survived longer in a zinc sulphate solution than embryos of the same age with an intact membrane. If the outer egg membrane impermeability were a major factor in preventing ammonia toxicity, all alevins would be instantly vulnerable at hatching. No sudden susceptibility to toxicants in newly hatched fish was observed in this study or in several others.

We can see no satisfactory explanation for the observed high resistance to ammonia and other toxicants during early developmental stages of teleosts. The higher resistance of sac fry than eggs to toxicants indicates that the egg membranes are not always protective barriers and that the explanation is more complex.

In our study, the susceptibility to ammonia developed during the transition from alevin to fry, toward the end of yolk absorption. This transition, although gradual, is probably more of a physiological change than the changes that occur at hatching. The newly hatched alevins are more "embryo" than "juvenile." They normally reside in the incubation gravels, have few voluntary responses to changes in their environment, and continue to develop by catabolizing their yolk. As the alevin develops and becomes prepared for emergence, susceptibility to some toxicants increases. The alevins are now more juvenile than embryo, even to the point of preemergent feeding as concluded by Dill (1967) for sockeye salmon alevins.

Our results indicate that rainbow trout embryos and alevins are safer from ammonia toxicity than are older salmonids (Burrows 1964; Larmoyeux and Piper 1973). A dramatic increase in the excretion of ammonia (Rice and Stokes in press) and sensitivity to ammonia appears to begin about the time the fry complete absorption of their yolk. Chronic exposure to ammonia would probably exert its greatest effects beginning at this stage also.

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NOTES

ADDITIONAL EVIDENCE SUBSTANTIATING EXISTENCE OF NORTHERN SUBPOPULATION OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

The northern anchovy, *Engraulis mordax* (Girard), ranges from Queen Charlotte Islands, British Columbia, to Cape San Lucas, lower Baja California. A study of variations in meristic characters (McHugh 1951) and genetic studies using serum transferrins (Vrooman and Smith 1971) generally support the hypothesis that three distinct subpopulations exist within this species' total geographic range. The dividing lines between subpopulations apparently occur at Point Conception, Calif. (delineating the northern and central elements), and at Cedros Island, central Baja California (delineating the central and southern elements).

Extensive spawning activity by the central and southern subpopulations is evidenced from the results of comprehensive egg and larvae surveys conducted since 1951 by the California Cooperative Oceanic Fisheries Investigations (Baxter 1967). Although these surveys suggest that the time-space distributions of spawning effort by these two subpopulations tend to overlap, evidently each achieves enough reproductive isolation to generate genetic differences between serum transferrins. Apparently, then, the central and southern subpopulations are capable of independently producing their own recruitment.

Until recently, the evidence for independent spawning by the northern subpopulation was not extensive. Ahlstrom (1968) noted that, in 1949 and 1950, anchovy larvae were found in moderate abundance off the Oregon coast. LeBrasseur (1970) indicated that a small number of larvae were taken in a 1958 survey of Queen Charlotte Sound, British Columbia. Waldron[1] stated that no eggs or larvae were taken in incidental samples off the Washington-Oregon coast in 1966 but that a few anchovy larvae were obtained during a comprehensive survey in the spring of 1967.

Such meager results might lead one to believe that the few larvae observed in northern waters were merely the result of incidental spawning activity. A conclusion might then be made that the northern subpopulation does not independently produce its own recruitment but relies instead upon an influx of anchovies from the two southern subpopulations.

In 1969, however, Richardson (1973) encountered such extensive numbers of anchovy larvae during a May-October survey of larval fishes off the Oregon coast (lat. 42°00'-46°30'N, coastline—long.129°30'W) that the above conclusions seemed to be refuted. Her results indicated the presence of a spawning stock of anchovies associated with the warm, near-surface waters of the Columbia River plume. Moreover, the peak of spawning seemed to be correlated with that period in summer when warm plume water (>14°C) was a dominant oceanographic feature.

Evidence from Length-Frequency Distributions

An analysis of age- and length-frequency distributions played a major role in determining stock structure for the Pacific sardine, *Sardinops sagax*. A similar analysis of length-frequency distributions was undertaken for the northern anchovy. The following review outlines the rationale and criteria applied in the sardine analysis and adapted for this study.

Early sardine investigators at first hypothesized that three subpopulations composed this species' total west coast population[2]. However, in addition to evidence of only sporadic spawning activity (Ahlstrom 1954), age- and length-frequency distributions obtained from the so-called northern subpopulation failed to reveal the presence of the most recently produced age-groups, i.e., the 0's, 1's, and 2's (Harry 1948). These ages, however, were often observed in samples from the central and southern subpopulations. The consistent absence of 0's from northern samples presumably confirmed a lack

[1]Waldron, K. D., Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash., pers. commun. 1971.

[2]A northern subpopulation supposedly ranged from British Columbia southward to central California, while central and southern subpopulations resided respectively off southern California and lower Baja California.

of independent spawning activity by that subpopulation of sardines (Harry 1949). The consistent presence of 0's, of course, would have indicated that independent spawning had occurred.

Figure 1 presents the length-frequency distributions analyzed in this study. These anchovy lengths were obtained from four exploratory fishing surveys conducted from Cape Flattery, Wash., to Yaquina Bay, Oreg., during 1966-67. These surveys occasionally encountered schools of anchovies containing small fish which became gilled in the meshes of the survey gear (Figure 2). It was speculated that these small anchovies were the result of recent spawning activity in the Washington-Oregon area.

To analyze these length distributions, one must first know the range of lengths associated with individuals belonging to age-group 0. Clark and Phillips (1952) indicated that 0-age anchovies begin entering the southern California live-bait fishery at lengths ranging from 5 to 9 cm. Miller (1955) stated that 0-age fish begin entering the southern California commercial fishery at 8.5-9.0 cm. Tillman (1972) concluded that anchovies are at least 6 mo old when they enter the commercially exploitable population at 9 cm. Figure 3 presents the ranges, medians, and median quartiles of the lengths of anchovy larvae obtained by Richardson (1973). These indicate that, in the northern subpopulation, 0-age anchovies approach 6 cm after 5 mo of growth. Thus, a length range of 0-9 cm should define those anchovies which resulted from spawning, at least, during the past 6 mo. This range was used to define the 0-age component in all length-frequency distributions.

Applying this criterion, the bar graphs of Figure 1 indicate that 0-age anchovies indeed were present in the northern subpopulation during the years surveyed. Lengths less than 4 cm were not found, but the 4-9 cm range composed, respectively, 11.6, 19.8, 87.0, and 39.0% of these four length-frequency distributions. The results shown for November-December 1966 and February 1967 are particularly striking, having major modes located respectively at 6 and 5.5 cm. These latter two distributions result from the facts that anchovies tend to school by size and that the later 1966 and early 1967 surveys primarily encountered schools of small fish. Therefore, following the rationale discussed at the beginning of this section, the presence of such juveniles would tend to confirm the

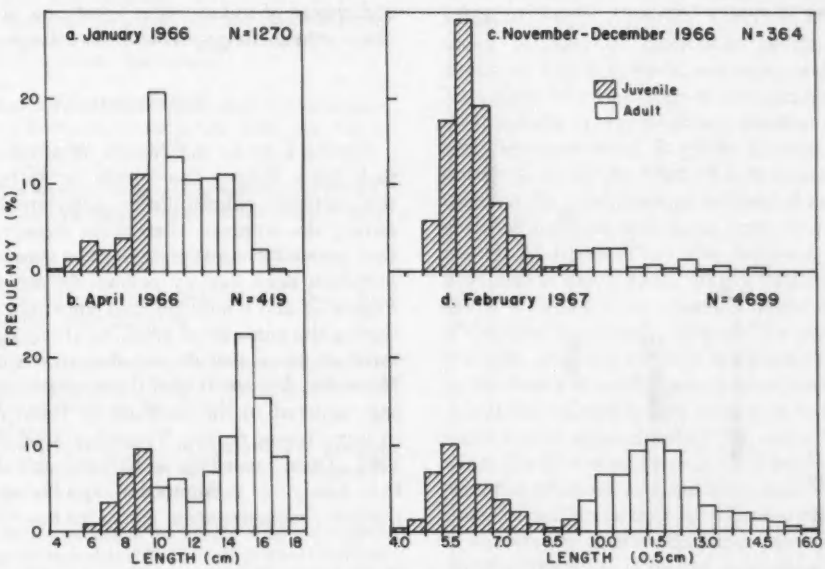
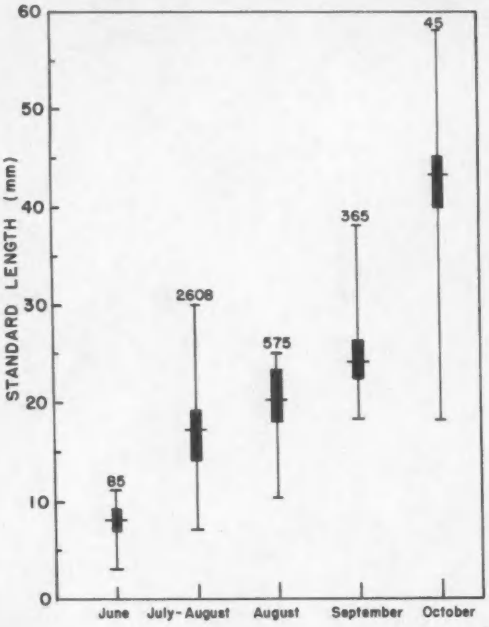


FIGURE 1.—Composite length-frequency distributions of juvenile and adult northern anchovy sampled off Washington-Oregon during 1966-67.

FIGURE 2.—Juvenile northern anchovy gilled in the meshes (½-¾ inch) of a mid-water trawl off the Washington-Oregon coast.



occurrence of independent spawning activity by the northern subpopulation of anchovies.

Discussion

Figure 1 gives the results of surveys which took place during the winter or spring. Since the northern subpopulation apparently spawns during the summer, then these figures indicate that spawning occurred during the summer which preceded each survey period. In other words, Figure 1a and b indicate that spawning occurred during the summer of 1965, resulting in recruitment of 0-age fish during January-April 1966. Moreover, Figure 1c and d indicate that spawning occurred in the summer of 1966, resulting in recruitment during November 1966-February 1967. Thus, according to Richardson's data and this analysis, independent spawning by the northern subpopulation seems to have occurred

FIGURE 3.—Ranges, medians, and median quartiles of lengths of northern anchovy larvae obtained during May-October 1969 off Oregon (Richardson 1973).

quite regularly rather than incidentally (occurring at least in 1965, 1966, and 1969).

Consequently, it is concluded that the presence of anchovies in northern waters does not represent a mere expansion of this species' geographic range—an expansion that well might have accompanied its recent fivefold increase in total population size. The previously mentioned genetic and meristic evidence, the results of recent larvae surveys, and the above length-frequency analysis would all seem to refute such a conclusion. Moreover, since this subpopulation was the mainstay of a substantive fishery for live bait during the 1940's (Pruter 1966), it seems to have been a persistent feature of the Washington-Oregon coast even before the dramatic expansion of the anchovy biomass which followed the demise of the sardine. Thus the weight of evidence seems to indicate that the northern subpopulation of anchovies is one of three independent population elements, all of which are capable of spawning and producing their own recruitment.

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COMMENT. INTRODUCTION OF *CODIUM* IN NEW ENGLAND WATERS

Genus *Codium* is one of the most common forms of seaweed found in almost every latitude but, until recently, has been absent from the east coast of North America. *Codium* attaches to rocks, pilings, old molluscan shells, and also shells of living oysters, scallops, and mussels. This algae has a number of common names, such as spaghetti grass, staghorn, deadman's fingers, and Japanese weed. It grows rapidly and often becomes so dense that it sometimes creates undesirable conditions on cultivated and natural shellfish beds, as well as in some other environments. At times it becomes buoyant enough to float and to carry along with it mollusks, to the shells of which it is attached. Mass mortalities of *Codium* are usually followed by quick decomposition, creating adverse conditions that result in the death of mollusks and other bottom forms.

No *Codium* was known to exist in New England waters until approximately the end of the 1950's, when the first specimens of *Codium fragile* were reported from several aquatic areas adjacent to Long Island. Since then it has become established in the waters of New England, spreading as far north as the State of Maine. According to a recent article (Quinn 1971) "It is now a dominant seaweed in the waters of Eastern Long Island and

can be found from Barnegat Bay, N.J., to Boothbay Harbor, Me."

Because of its wide distribution in the new environment, *Codium* now causes serious impact on local ecology and also creates serious problems on shellfish beds. There is some question, naturally, as to when the first introduction of this algae occurred and how this somewhat undesirable "immigrant" was brought into our eastern waters. Quinn (1971) quotes Mueller, who, apparently without any evidence, speculates that "It was imported on the backs of oysters from Europe and Japan." Since I am responsible for the introduction of the European oyster, *Ostrea edulis*, into the waters of New England (Loosanoff 1951, 1955), I wish to comment on this matter.

The European oysters were brought to Long Island Sound in October 1949, when I was the Director of the United States Bureau of Commercial Fisheries Biological Laboratory at Milford, Conn. The shipment was comprised of approximately 2 bushels of the mollusks, ranging in age from 1 to 3 yr. They were shipped in a vegetable compartment of a large refrigerator on a Holland-American Line passenger ship and spent about 13 days in transit.

The introduction of *O. edulis* was made in accordance with the decision reached after my consultations with members of the shellfish industry, as well as with leading marine biologists of that period, including Paul S. Galtsoff of the United States Bureau of Commercial Fisheries and Thurlow Nelson of Rutgers University. Federal authorities approved the importation and the Director of the State of Maine Sea and Shore Fisheries, who was extremely interested in planting European oysters into those waters, gave me a small sum of money to pay for that shipment. The latter fact, obviously, discredits Mueller's statement, quoted by Quinn, that "The oysters were removed from Milford and Woods Hole without permission and introduced into local waters."

In introducing European oysters it was our desire to establish a second commercial species of bivalves in the waters of Maine. At that time only one mollusk, the soft-shell clam, *Mya arenaria*, was commercially utilized in that region. However, because of extremely heavy mortality among the *Mya* in the mid-1940's, this species became almost extinct for a period of several years. As a result, many shore communities which depended upon soft-shell clam fisheries were deprived of the chief means of their livelihood. Therefore, it seemed logical to me that a second shellfishery should be developed in those waters, namely that of *O. edulis*. If successful such a development would enhance the economy of the region. *Ostrea edulis* was chosen for the cold waters of Maine because, in addition to its high quality as human food, it is able to propagate at a considerably lower temperature than the American oyster, *Crassostrea virginica*.

In bringing the oysters from Europe, I dealt with my friend, Peter Korringa, who is now Director of the Netherlands Institute for Fishery Investigations. At that time he was already considered one of the world's leading shellfish experts. Being fully aware of the possibility of introducing undesirable exotic species which might accompany the European oyster, our group of American biologists, as well as Korringa, decided to take precautionary measures considered sufficient to prevent such an occurrence. The problem was discussed at great length in correspondence between Korringa and myself, and I still have in my files several of Korringa's letters attesting to this exchange. For example, in his letter of March 1949, Korringa wrote "I can kill any germs in the shell by disinfecting the consignment before shipment." In May of the same year he wrote again "I will disinfect very carefully every oyster we ship you with the chemicals we find satisfactory to that end." In his recent letter to me, dated 27 November 1973, Korringa wrote as follows: "I suggested to treat the oysters by bathing them in a mercury solution, using the organic fungicide we used on large scale against infection with shell disease. This kills hundred procent all organisms on the outside of the shell which cannot withdraw in a hermetically closed shell. You see from my correspondence that I have treated the oysters with this disinfectant before shipping them. Therefore I feel sure that *Codium fragile* cannot have been introduced in the American Atlantic waters with our oysters."

When the oysters arrived at Milford, they were again carefully examined, washed with fresh water, and dipped in a weak solution of copper salt. At that time, however, we were not concerned as much with the introduction of *Codium*

as we were afraid of bringing along a highly destructive fungus causing so-called "oyster shell-disease." Because of Korringa's assurance, however, we were quite certain we would eliminate this and any similar dangers.

The small shipment of European oysters was later divided into two parts, one taken to the U.S. Bureau of Commercial Fisheries Laboratory at Boothbay Harbor, Maine, where some of the oysters were suspended off the dock, the other part kept in Milford Harbor, remaining there under the observation of my associates and me for several years. Not in a single instance did I, other members of Milford Laboratory, or John B. Glude, Director of the U.S. Bureau of Commercial Fisheries Laboratory at Boothbay Harbor, or his colleagues, notice or report to me the presence of *Codium* on the oyster shells. Therefore, considering the chemical treatment that was given the oysters before they were placed in open American waters and because of the results of our long-term observations of these oysters at both Milford and Boothbay Harbor, it is improbable that *Codium* was brought into the waters of New England "on the backs of the European oysters."

There are several much more plausible explanations as to the way *Codium* was introduced to our Atlantic coast. In my opinion, it was brought into our waters during World War II. At that time, to avoid being torpedoed by German submarines along the open Long Island coast, many freighters coming from Europe to the port of New York traveled through the well-protected inside passage—Long Island Sound. At times, these vessels were so numerous that many of them had to be anchored in Long Island Sound for several weeks before they could be unloaded at New York piers. I was then engaged in the study of plankton of Long Island Sound—in relation to propagation of oysters—running, sometimes, 14-h sampling series from a small boat. Several of our collecting stations were then located on the Bridgeport and New Haven oyster beds where seed oysters were dredged each fall and planted on cultivated beds of Long Island, Rhode Island, Massachusetts, and even Maine (Loosanoff 1966).

To avoid the wind and heavy wave action we would usually position our boat on the lee side of anchored freighters. Often we were so close to those vessels that we could converse with members of their crews. Many of these ships were of European registry and, because of the war, most of them were not able to undergo proper bottom cleaning for several years. As a result of this neglect, the ship bottoms were covered with heavy layers of marine fouling organisms. Sometimes such layers, as had been reported by Woods Hole investigators, were as much as 2, or even 3, feet thick (Woods Hole Oceanographic Institution 1952). The fouling mass was composed of many forms, including mussels, tunicates, and, no doubt, a variety of other organisms. The *Codium* was also present and sometimes clearly visible. While the freighters were riding at anchor, frequently large chunks of the fouling mass broke off and fell to the bottom of the Sound. We witnessed this phenomenon on numerous occasions.

Thus, it appears logical that *C. fragile* gained entrance into the waters of eastern United States from the bottoms of European freighters during World War II. This possibility, however, seems to be ignored; the blame is placed instead, directly or indirectly, on a small, properly handled shipment of European oysters which was brought from Holland to Milford in 1949 (Quinn 1971).

It may be mentioned, in conclusion, that, as originally planned, the European oysters planted in Boothbay Harbor not only survived in the new environment but reproduced under a new set of ecological conditions and became firmly established within a large area (Welch 1966). Therefore, these excellent "immigrants" may soon become the second commercial shellfish crop of Maine. Secondly, *Codium*, although a nuisance and a highly undesirable invader in some respects, and for introduction of which we claim no "credit," may be a welcome addition to localized biosystems by providing extensive, rich-in-food, protective nursery areas to the advanced larval stage and juveniles of many fishes and of such important species of commercial invertebrates as the American lobster, *Homarus americanus*, and the blue crab, *Callinectes sapidus*.

I wish to thank John B. Glude for reading this manuscript and offering constructive suggestions.

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ERRATA

Fishery Bulletin, Vol. 72, No. 4

KENNEDY, V. S., W. H. ROOSENBURG, M. CASTAGNA, AND J. A. MIHURSKY, "*Mercenaria mercenaria* (Mollusca: Bivalvia): Temperature-time relationships for survival of embryos and larvae," p. 1160-1166.

1) Page 1161, right column, line 13, correct line to read:
(25 mm) in an 8 × 11 matrix (see Figure 1,

2) Page 1163, the figure legends for Figures 2 and 3 were switched in printing. The legend for Figure 2 should be under the second drawing in the left column and that for Figure 3 should be under the drawing in the right column.

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